

Generating and filtering major phenotypic novelties: neoGoldschmidtian saltation revisited

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ABSTRACT

Further developing a controversial neoGoldschmidtian paradigm that we first published in 1994, we here narrowly define saltational evolution as a genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage termed a prospecies (the 'hopeful monster' of Richard Goldschmidt). Of several saltational and parasaltational mechanisms previously discussed by us, the most directly relevant to evolutionary–developmental genetics is dichotomous saltation, which is driven by mutation within a single ancestral lineage. It can result not only in instantaneous speciation but also in the simultaneous origin of a profound phenotypic novelty more likely to be treated as a new supraspecific taxon. Saltational events form unusually long branches on morphological phylogenies, which follow a punctuated equilibrium pattern, but at the time of origin they typically form zero length branches on the contrastingly gradualistic molecular phylogenies. Our chosen case-studies of heterotopy (including homeosis) and heterochrony in fossil seed-ferns and extant orchids indicate that vast numbers of prospecies are continuously generated by mutation of key developmental genes that control morphogenesis. First principles suggest that, although higher plant mutants are more likely to become established than higher animals, the fitness of even plant prospecies is in at least most cases too low to survive competition-mediated selection. The establishment of prospecies is most likely under temporary release from selection in environments of low biotic competition for resources, followed by honing to competitive fitness by gradual reintroduction to neoDarwinian selection. Unlike neoDarwinism alone, this two-phase evolutionary paradigm is consistent with the recent results of (a) whole-genome sequencing, which have revealed a surprisingly small total number of genes per model species, and (b) of Quantitative Trait Locus analyses, which indicate that major phenotypic features are determined by one or two homeotic genes of major phenotypic effect and only a handful of genes of lesser effect. Evolutionary–developmental genetics has already proved beyond reasonable doubt the credibility of the initial 'generative phase' of the neoGoldschmidtian hypothesis (though further investigation is needed of the effects of canalisation and epigenesis following both gain and loss of function). Unfortunately, far fewer data are currently available to test the subsequent 'establishment phase'; this deficiency places a premium on monitoring the ecological progress of many prospecies, in both artificial and natural

habitats. Saltation is superior to classical neoDarwinian selection in removing the highly improbable requirement to drive alleles to fixation in large populations, explaining sympatric speciation, allowing lineages to cross otherwise lethal fitness valleys, giving key evolutionary roles to pre-adaptation and exaptation rather than adaptation, and providing a direct causal explanation of the qualitatively different levels of morphological divergence that underpin the Linnaean hierarchy.

7.1 Introduction

On the theory of natural selection we can clearly understand the full meaning of that old canon in natural history, 'Natura non facit saltum.' This canon, if we look only to the present inhabitants of the world, is not strictly correct, but if we include all those of past times, it must by my theory be strictly true.

(Jones, 1999: 189)

In the summer of 1993, we attempted to synthesise a new 'supraDarwinian' paradigm in the evolutionary biology of vascular plants for an edited volume entitled *Shape and Form in Plants and Fungi* (Bateman and DiMichele, 1994a). Our wide-ranging discussion primarily concerned the credibility of, and the evidence for, non-gradual evolution of plant form that did not rely on classic neoDarwinian mechanisms – in other words, on directional or disruptive selection acting via adaptively-driven fixation of mutant alleles and traced via Hardy–Weinberg equilibria within large panmictic populations (for clear expositions of these principles see Ridley, 1996; Patterson, 1999). We ultimately reached the following conclusions (p. 91):

It has long been accepted that the fundamental unit of evolutionary change is the gene but that such changes are mediated via the phenotype of the host organism (the replicators and interactors respectively of Dawkins, 1982, 1986, 1989). Recent studies of [homeotic] gene expression in plants (e.g. Coen, 1991; Coen and Carpenter, 1992; ...) provide a vital causal link between genotype and phenotype – replicator and interactor – that allows reciprocal illumination between these two contrasting manifestations of the evolutionary process. [Attributes of homeotic] genes can be coded cladistically in order to make the crucial distinction between primitive and derived states and, as we have shown, the resulting cladograms can be used to test competing hypotheses of underlying evolutionary mechanisms. Despite recent advances (Chasan, 1993), biologists have been surprisingly slow to combine relevant concepts of gene expression, developmental control, phylogeny reconstruction, ecological filtering of phenotypes, and evolutionary theory into a truly integrated evolutionary synthesis. This problem has been exacerbated by over-enthusiastic generalisation from parochial studies of a few 'flagship' species to all-embracing evolutionary theories. Nonetheless, we are confident that future syntheses will confirm our opinion that plants have their own distinct approach to the evolution of shape and form.

These deliberately provocative statements, and our subsequent reformulations of various aspects of the paradigm (Bateman, 1994, 1996, 1999a, b; Bateman and

DiMichele, 1994b; DiMichele and Bateman, 1996; Bateman *et al.*, 1998) attracted disappointingly few commentaries (e.g. Rutishauser, 1995; Erwin, 2000; Tucker, 2000, 2001) prior to this volume (Baum and Donoghue, 2002; Cronk, 2002; Theissen *et al.*, 2002). Our 1994 synthesis was very much a product (or perhaps a victim?) of its time. Despite a few eloquent dissidents, often from the palaeobiological community (most notably Gould and Lewontin, 1979; cf. Morris, 2001), evolutionary theory was (and is) dominated by strict neoDarwinians whose perspectives differed only in fine detail: all relied on the mathematically modelled gradual spread through populations of alleles that engendered subtle modifications of phenotype, increasing in frequency through directional or disruptive selection mediated primarily by competition (for recent examples, the latter extensively quoted in this chapter, see Dawkins, 1986, 1989; Maynard Smith, 1989; Maynard Smith and Szathmary, 1995; Ridley, 1996; Jones, 1999). Adaptation was used, often unthinkingly, as a null hypothesis for most specific evolutionary transitions (Bateman and DiMichele, 1994a) and for evolutionary radiations (Bateman, 1999a), however limited and ambiguous the evidence for levels of selection capable of inducing genuine speciation. And botanists had surprisingly little to say on such lofty matters, preferring to co-opt, with at best minor modifications, theories that were essentially zoocentric.

However, in the field of developmental genetics, genuine breakthroughs in understanding the control of metazoan body plans through the homeotic Hox genes (e.g. Slack *et al.*, 1993; Valentine *et al.*, 1999; Mindell and Meyer, 2001) had been accompanied by the elucidation of the classic ABC model of angiosperm flower development through studies of *Arabidopsis* and *Antirrhinum* (e.g. Coen and Meyerowitz, 1991; Theissen *et al.*, 1996, 2002; Cubas, 2002). Also, the increasingly perceived possibility of harnessing these emerging insights in developmental genetics for evolutionary studies prompted the benchmark plant evo-devo conference at Taos, New Mexico in the summer of 1993 (summarised by Chasan, 1993, as cited by us in the above quote).

Eight years on, it seems appropriate to assess how much (or indeed how little) progress has been made toward the crucial goal of formulating a holistic evolutionary paradigm that encompasses the origin, phylogenetic context and ecologically-mediated fates of mutations in key morphogenetic genes.

7.2 SupraDarwinian evolutionary mechanisms

7.2.1 NeoGoldschmidtian saltation

Geneticists were once so impressed with mutation as to suggest that new forms of life arise not through the accumulation of small changes but in great leaps. Evolution was due to the instability of genes and genetics had, perhaps, destroyed Darwin's idea. It had not: mutation is the fuel rather than the engine of biological advance. The process involves mechanisms undreamed of in the science's first days.

(Jones, 1999: 147)

In his notorious evolutionary tome *The Material Basis of Evolution*, the Berkeley-based developmental zoo-geneticist Richard Goldschmidt (1940) argued that

'systemic mutations' (large-scale chromosomal rearrangements) altered early developmental trajectories to generate, across a single generation, 'hopeful monsters' – teratological lineages of phenotypes radically different from their parents. By chance, some hopeful monsters possessed high levels of fitness that enabled their persistence as new lineages of great evolutionary significance. It was not difficult for aggressive advocates of the neoDarwinian *New Synthesis* to fatally undermine Goldschmidt's thesis by discrediting his concept of macromutations and mathematically 'proving' the improbability of hopeful monsters instantaneously acquiring competitively high fitness. Consequently, occasional attempts to resurrect various aspects of Goldschmidt's saltational paradigm (e.g. Waddington, 1957; Croizat, 1962; van Steenis, 1976; Gould, 1982; Arthur, 1984; Orr, 1991; Bateman and DiMichele, 1994a), or to re-assess the generally overlooked contributions of Goldschmidt's intellectual predecessors (e.g. see the discussion of the views of influential German plant morphologist W. Troll as portrayed by Kaplan, 2001b), attracted relatively little attention.

As few evolutionary biologists provided explicit definitions of saltational (or 'saltatory') evolution, the term has been used to encompass a wide range of often conflicting concepts. In our previous attempt to define (and thus recognise) saltational evolutionary events (Bateman and DiMichele, 1994a), we immediately excluded from consideration all non-genetic ecophenotypic and ontogenetic variation within species. We also emphasised the related difference between the concept of a *teratos* – an individual possessing a radically different morphology from its immediate ancestor(s) irrespective of the underlying causal mechanism – and Goldschmidt's concept of a '*hopeful monster*', where a genetic cause of the morphological discontinuity is assumed and non-heritable causes are specifically excluded (Table 7.1).

Saltation requires a substantial change in phenotype between ancestor and descendant. As developmental genetic studies have conclusively demonstrated that

Table 7.1 Formal definitions of key terms relating to exceptionally rapid speciation (modified after Bateman and DiMichele, 1994a: 66–67)

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|--------------------------------|--|
| <i>Saltation</i> : | a genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage. |
| <i>Porosoltation</i> : | a genetic modification that is expressed as a profound phenotypic change across two to several generations and results in a potentially independent evolutionary lineage. |
| <i>Dichotomous saltation</i> : | saltation driven by mutation of at least one gene within a single ancestral lineage. |
| <i>Reticulote saltation</i> : | saltation driven by allopolyploidy and thus blending the entire genomes of two ancestral lineages. |
| <i>Teratos</i> : | an individual showing a profound phenotypic change from its parent(s) irrespective of whether the underlying cause is genetic or ecophenotypic (plural, <i>teroto</i>). |
| <i>Hopeful monster</i> : | an individual showing a profound phenotypic change from its parent(s) that demonstrably reflects a genetic modification. |
| <i>Toxonomic species</i> : | one or more (typically many more) populations separated from all other comparable populations by phenotypic, and putative genotypic, discontinuities that are believed to reflect one or more isolating mechanisms operating over a considerable period of time. |
| <i>Prospecies</i> : | a putatively recently evolved lineage possessing the essential intrinsic properties of a taxonomic species but yet to achieve levels of abundance and especially of longevity acceptable to practising taxonomists. |

magnitude of phenotypic change engendered by a modification of a specific gene is decoupled from the magnitude of the change in the genome itself, quantification of the degree of phenotypic change is clearly the most appropriate criterion for saltation. Increased overall complexity is definitely not a requirement; indeed, current evidence suggests that saltational events which suppress developmental genes and consequently reduce morphological complexity are far more common than saltational events which increase overall complexity (cf. Kellogg, 2002).

In 1994 we abrogated our responsibility to define the profoundness of morphological transition necessary to pass the threshold of saltation, and we continue to do so here. The primary expectation is of a high degree of phenotypic divergence in a well-sampled phylogenetic (and perhaps phenetic: DiMichele *et al.*, 2001) study that allows reasonably accurate comparison of degrees of morphological divergence, which should be considerable, and of sequence divergence, which should be minimal in the immediate aftermath of the saltation event but, unlike morphology, changes progressively and gradually thereafter (Bateman, 1999a).

Rate of evolutionary change is a second key criterion for saltation. Some authors (e.g. Ayala and Valentine, 1979) chose to define saltation as a period when the temporal rate of evolution (change/time) is substantially greater than the long-term average within the lineage. However, this definition is more appropriately discussed in the context of evolutionary radiations (Bateman *et al.*, 1998; Bateman, 1999a), as it encompasses not only our saltation *s.s.* but also several contrasting mechanisms of rapid evolutionary change that we prefer to collectively term 'parasaltational' (see Section 7.2.2). We believe that saltation is better defined by generation time than absolute time, and hence argue that a saltational change must occur across a single generation. Although hopeful monsters will have a much greater likelihood of retaining their novel phenotype if they become reproductively isolated from the parental population, particularly if the isolation reflects intrinsic properties of the monsters rather than mere *ad hoc* spatial separation (i.e. sympatry rather than allopatry), new lineages can in theory become established even in the absence of reproductive isolation (Arthur, 1984). This criterion is therefore ancillary to, rather than inherent in, *saltation*, which can now be defined more precisely as a genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage (Table 7.1).

A single hopeful monster has by definition a minimal geographical and ecological distribution; if also reproductively isolated, in principle it fulfils the criteria required for a biological species *sensu* Mayr (1963). However, in practice the hopeful monster is unlikely to be awarded specific rank by a taxonomist, who requires a *taxonomic species* to demonstrate a degree of historical tenacity by establishing a sizeable population that persists through many generations. This is a reasonable *modus operandi*, as most lineages resulting from saltation undoubtedly fail to survive beyond a single generation, and very few exceed ten or a hundred generations; these typically ephemeral entities are better described as *prospecies* (Table 7.1). Note that there is no intrinsic biological distinction between *prospecies* and taxonomic species; taxonomic species can only be distinguished retrospectively, on the basis of their far greater temporal continuity and spatial extent. Also, an ageist bias is evident in most taxonomic treatments. A species inevitably has an origin, an acme and ultimately an extinction that are defined both temporally and spatially (Levin, 2000, 2001).

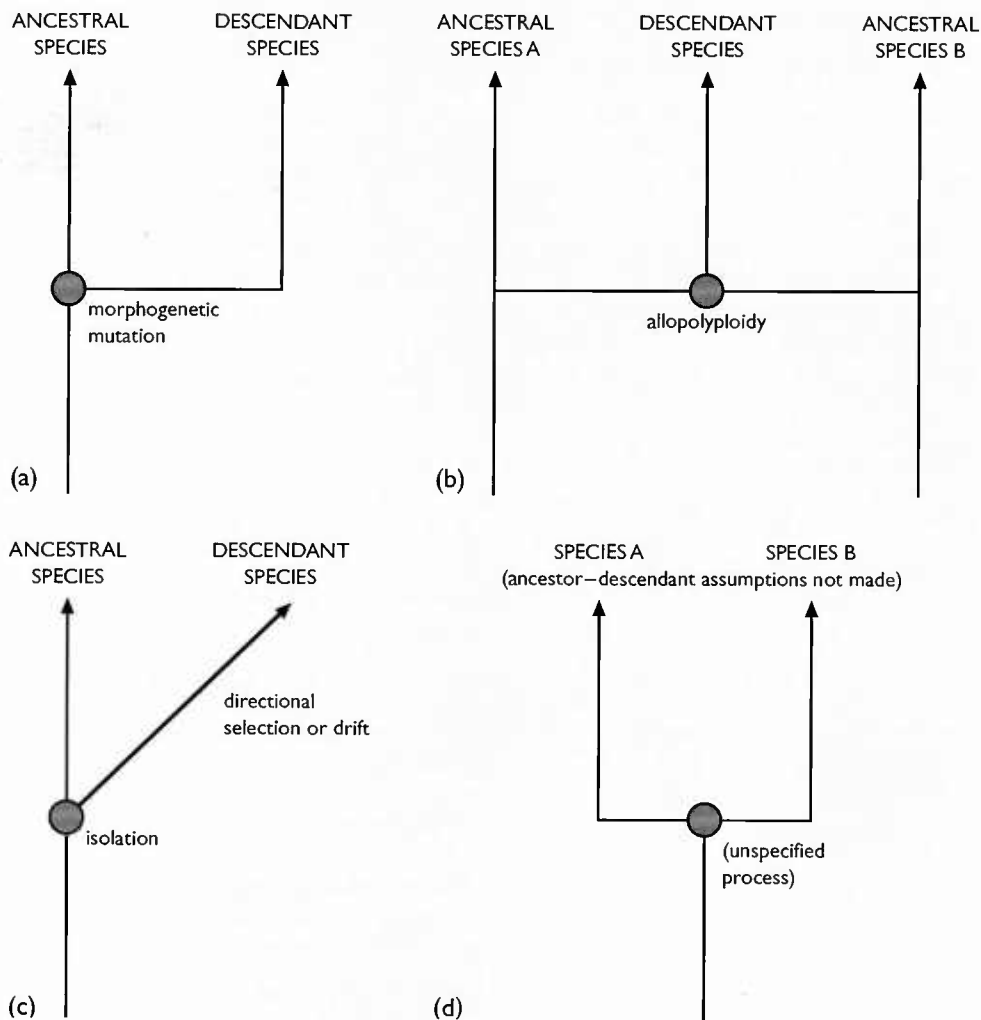


Figure 7.1 Comparison of contrasting evolutionary patterns. Dichotomous saltation (a) shows instantaneous divergence of descendant from ancestor via a mutation in a key gene controlling morphogenesis. Reticulate saltation (b) also occurs instantaneously via allopolyploidy but blends two parental genomes. Directional selection or drift (c) cause gradual divergence of the descendant following its isolation. Cladistic representations of speciation (d) assume no ancestor–descendant relationships and specify no underlying process.

However, in practice, taxonomists are more reluctant to recognise as a full species a rare but putatively recent, expanding population than a rare but putatively long-lived, senescent population that represents far greater historical continuity.

Thus far, we have considered only mutationally-driven saltation. Other modes of genotypic change rely on mixing pre-existing genes from individuals of two species (hybridisation) or on duplicating a complete set of pre-existing genes in a single individual (autopolyploidy), but neither phenomenon generates a new reproductively

Table 7.2 Examples of parasaltational evolutionary mechanisms, with relevant literary sources

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| <i>(o) Reticulate processes that combine formerly disparate lineages</i> | |
| 1. Hybridisation* | Stace, 1989, 1993; Goodnight, 1995, 1999; Rieseberg <i>et al.</i> , 1995; Wendel <i>et al.</i> , 1995; Rieseberg, 1997; Vogel <i>et al.</i> , 1999; Rieseberg and Burke, 2001 |
| 2. Endosymbiosis | Margulis, 1993; Martin and Schnarrenburger, 1997 |
| <i>(b) Processes intrinsic to the behaviour of the genome</i> | |
| 3. Homeosis* | Raff and Kauffman, 1983; Arthur, 1984, 2000; Kauffman, 1993; Wray, 1995; Albert <i>et al.</i> , 1998 |
| 4. Neutral theory | Kimura, 1983, 1991 |
| 5. Nearly neutral theory | Ohta, 1992, 1995 |
| 6. Adaptive mutation | Foster and Cairns, 1992; Shapiro, 1997, 2002 |
| 7. Molecular drive | Dover, 1982, 2000 |
| 8. Meiotic drive | Pomiankowski and Hurst, 1993; McVean and Hurst, 1997 |
| 9. Multiple codes | Trifonov, 1997 |
| 10. Chromosomal rearrangements | Prescott and DuBois, 1996; Hoffman and Prescott, 1997 |
| 11. Transposon-induced deactivation | Wessler <i>et al.</i> , 1995; Federoff, 2000; Walbot, 2002 |
| <i>(c) Processes emergent from genetic control of development</i> | |
| 12. Epigenesis | Goodwin and Saunders, 1992; Jablonka <i>et al.</i> , 1992; Goodwin, 1994; Jablonka, 1994; Jablonka and Lamb, 1995 |
| 13. Epistasis | Papers in Wolf <i>et al.</i> , 2000 |
| <i>(d) Processes directly linked to the ecological spread of genetic novelties</i> | |
| 14. Drift | Templeton, 1989; Gillespie, 1991; Barrett and Pannell, 1999; Patterson, 1999 |
| 15. Shifting balance | Wade, 1992; Goodnight, 1995; Whitlock, 1997; Wade and Goodnight, 1998; Mallet and Joron, 1999 |
| 16. Correlated selection | Price <i>et al.</i> , 1993 |
| 17. Species selection | Gould, 1986; Eldredge, 1989 |
| 18. Clade selection | Williams, 1992 |

Note: * = events that are also potentially saltational.

isolated evolutionary lineage across a single generation. However, by first mixing genes of two lineages and then duplicating the entire heterogeneous genome, thus restoring fertility, allopolyploidy does immediately generate a novel lineage that is often also reproductively isolated (Stebbins, 1971; Stace, 1989, 1993; Thompson and Lumaret, 1992; Wendel *et al.*, 1995; Rieseberg, 1997; Vogel *et al.*, 1999; Rieseberg and Burke, 2001; Wolfe, 2001). Similarly, the endosymbiotic origins of mitochondria and plastids (Margulis, 1993; Martin and Schnarrenberg, 1997) can only realistically be viewed as unusually profound reticulate saltation events.

Thus, Bateman and DiMichele (1994a) concluded that two distinct modes of saltation exist (Table 7.1, Figure 7.1). In *dichotomous saltation* (Figure 7.1a), hopeful monsters originate by mutation; one new daughter lineage diverges instantaneously from the ancestral lineage, thereby forming a dichotomous pattern that can in theory be resolved cladistically (as can the gradual divergences implicit in directional selection or drift: Figure 7.1c). However, in *reticulate saltation* (Figure 7.1b), allopolyploidy combines elements from two ancestral lineages; the resulting reticulate pattern cannot be adequately accommodated in a dichotomous cladogram (note that the cladistic method is neutral regarding both ancestor–descendant and process-based interpretations: Figure 7.1d). The general absence of mutation in reticulate saltation restricts the potential range of immediate phenotypic innovation, so that speciation events are less likely to coincide with the origins of supraspecific taxa than is the case in dichotomous saltation (cf. van Steenis, 1976; Arthur, 1984; Stace, 1993; Wolfe, 2001). Thus, dichotomous saltation is of greater relevance to evolutionary–developmental genetics, though reticulate saltation also remains an important evolutionary process as each such event is on average more likely to generate viable phenotypes capable of establishing long-lived lineages.

7.2.2 The diversity of parasaltational mechanisms

Quite how [mimetic] insects traversed the valley of death – in a sudden leap, with a single gene pushing them most of the way, or by small changes getting together by accident – is not clear.

(Jones, 1999: 160)

The narrowness of our definition of saltation excludes several evolutionary mechanisms, most under-explored, which are capable of causing speciation events that are exceptionally rapid but not instantaneous. These are more appropriately described as *parasaltational* (Table 7.1).

First, the stringent requirement for both genotypic and phenotypic change across a single generation excludes from strict saltation most mutations of recessive alleles; here, the genotypic change can only be expressed in the F1 generation in rare cases where a recessive mutation in a germ cell precursor is followed by self-fertilisation involving two gametes, each of which carries the mutation (Arthur, 1984). Hybridisation *per se* is similarly excluded (cf. Abbott, 1992; Rieseberg *et al.*, 1995).

Specifying instantaneous speciation also rules out evolutionary scenarios that focus on populations of small effective sizes, typically due to reduction induced by various forms of environmental stress, by a marginalisation event leading to parapatry, or by a vicariance event leading to allopatry (Levinton, 1988). The neutral

theory (Kimura, 1983, 1991) and subsequent nearly neutral theory (Ohta, 1992, 1995) predict that random sampling effects alone can lead to allele fixation or extinction in small populations, largely independent of selective advantage. Various reformulations of Wright's (1932, 1968) shifting balance theory (Lewis, 1962, 1966, 1969; Levin, 1970, 1993, 2000; Templeton, 1982, 1989; Carson, 1985; Lande, 1986; Wade, 1992; Whitlock *et al.*, 1995; Whitlock, 1997; Wade and Goodnight, 1998; Mallet and Joron, 1999; Wolf *et al.*, 2000; cf. Coyne *et al.*, 1997) predict that random genetic drift in small populations can temporarily override selective pressures on alleles, thereby allowing populations to cross non-lethal valleys on the adaptive landscape to the slopes of another peak, which is then climbed by classic neoDarwinian selection. Drift is in theory expressed most profoundly when it disrupts and destabilises developmental homeostasis (Levin, 1970; see also Patterson, 1999). Although most such populations fail, this process provides an occasional opportunity to substantially re-organise the developmental programming under conditions of low infraspecific competition and high physical stress ('catastrophic selection' *sensu* Lewis, 1962, 1966, 1969; Carson, 1985).

Shifting balance scenarios are consistent with evolutionary patterns that were termed 'punctuated equilibria' by Eldredge and Gould (1972) – long periods of stasis followed by brief periods of rapid phenotypic change. Vermeij (1987) extended the ecological component of these scenarios, arguing that periods of stasis reflect neoDarwinian processes and are punctuated by ecosystem disruptions that locally reduce selection pressure, species diversity and population sizes. Each such disruption allows escalation – a brief interval of intense competition to fill the vacated niches that increases the fitness of the competitors. Many of these observations apply equally well to populations that are very small, not because they have recently declined into an apocryphal 'bottleneck' but because they have just evolved by saltation – we will return to them later. Other explanations of punctuational patterns require differential survival of lineages, focusing on selection among species (Gould, 1986; Levinton, 1988; Gould and Eldredge, 1993) or even among clades (Williams, 1992).

7.3 Cladistic tests of evolutionary hypotheses

Cladistics, a German invention, has strict rules and a complex vocabulary. It can, if not carefully used, give erratic results and is still filled with argument about just what should be plugged into its analyses. It has, nevertheless, transformed our view of the world.

(Jones, 1999: 371)

In 1994, we felt obliged to outline the basic principles and methodology of cladistics before discussing its relevance to saltation theory. Presenting this background is no longer necessary, given the pre-eminence since achieved by cladistic techniques for reconstructing phylogenies. However, it is worthwhile restating our suggested use of cladograms for falsifying saltational hypotheses, and reviewing cladistic falsification of adaptation and exaptation in the light of increasing use of mapped quantitative variables for ecological interpretations (see review volumes by Harvey and Pagel, 1991; Harvey *et al.*, 1996; Silvertown *et al.*, 1997). Also, the rapid and profound

switch during the last decade from cladistic analyses based on morphology to those based on increasingly profligate DNA sequence data requires further consideration (cf. Bateman, 1999a; Chase *et al.*, 2000). Phylogenies can in practice be reconstructed using sequence data alone, but evolution can be understood only by relating genotype explicitly to phenotype.

7.3.1 Falsification of adaptation and exaptation

The number of morphological cladistic analyses of plants leading to interpretations of underlying causal mechanisms remains surprisingly small; numbers began to rise during the 1990s, but then plateaued as sequence matrices replaced morphology. Most such examples focused on adaptation (for early examples see Coddington, 1988; Donoghue, 1989; Maddison, 1990; for reviews see Harvey and Pagel, 1991; Harvey *et al.*, 1996; Silvertown *et al.*, 1997), and require three important codicils:

- 1 Many traits are likely to be *adaptive* (increase the perceived overall fitness of the organism) but far fewer are identifiable as *adaptations* that evolved via natural selection to fulfil a specific function. Despite many published criticisms, this key distinction is still often overlooked.
- 2 Morphological cladistic analyses by definition employ 'form' as characters, but rarely include explicit functions (cf. Lauder, 1990). Fortunately, this is not a serious handicap to interpretation, as particular functions can be plotted on a cladogram *a posteriori* (we discuss this procedure, strictly termed 'mapping', in more detail below).
- 3 When attempting to infer evolutionary process from cladistic pattern, it is only possible to state that a particular evolutionary process is *consistent with* a particular phylogenetic pattern. *Demonstrating* such a correlation requires additional biological data that are not appropriate for coding into the original cladistic matrix.

To be consistent with a hypothesis of adaptation, a particular form (represented as one or more character-state transitions on the morphological cladogram) and a particular function (mapped *a posteriori*) must evolve on the same branch of the cladogram. A form appearing below the postulated function on the cladogram is consistent with a hypothesis of exaptation; the form either evolved non-adaptively, or evolved adaptively but for a different function, only later acquiring its present function. A form appearing above the putative function on the cladogram refutes the hypothesis of positive correlation and thus of any causal relationship. Arrangements of form and function consistent with adaptation or exaptation are not positive proof of such hypotheses; rather, the value of the cladograms is negative, allowing falsification of postulated correlations.

7.3.2 Falsification of transference of function

This logic of transitional correlation also underpins the test of transference of function proposed by Baum and Donoghue (2002; also D. Baum, pers. comm. 2001), where the phylogenetic distribution of a particular function is mapped relative to

two or more non-homologous structures known to fulfil the function across the clade under scrutiny. Polymorphism of function in the hypothetical ancestor, or the presence of species where neither structure fulfils the function in question, both refute the hypothesis of transfer of that function from one structure to the other during the evolution of the clade. As with tests of adaptation and exaptation, the *a priori* hypothesis is conclusively refuted by a negative correlation, but is not proven by a positive correlation.

7.3.3 Falsification of saltation

Bateman and DiMichele (1994a) adopted and amended the logic of phylogenetic falsification to develop a cladistic test of non-adaptive, saltational hypotheses. The emphasis switches from demonstrating the simultaneous origin of a character state and its presumed adaptive function to demonstrating the simultaneous origin of several developmentally correlated character states. This, in turn, focuses attention on long branches – those supported by several morphological character-state transitions – and requires a literal (and thus somewhat philosophically controversial) interpretation of the cladogram as an evolutionary history. In this scenario, potentially developmentally correlated characters changing simultaneously on the cladogram are assumed to have changed simultaneously during evolution, most probably as the direct or indirect consequence of a single mutation event. In other words, saltation is regarded as the null hypothesis to explain particular long branches in morphological cladograms.

The credibility of this test is heavily dependent on the density of species sampling. Ideally, all known species in the chosen clade, both extant and extinct, should be sampled and coded in order to maximise the probability of dissociating multiple character-state transitions on a single branch. A more pragmatic approach would be to analyse the readily obtained species initially and then add other relevant species as they become available, as a secondary test of the initial saltational hypothesis (Bateman and DiMichele, 1994a, Figure 3).

There are several potential difficulties with using long branches in morphological trees as circumstantial evidence of saltation events:

- 1 Some manuals of morphological cladistic analysis state that morphological characters which are potentially developmentally correlated fail the cladistic requirement for independence and hence should be reduced to a single character prior to tree-building. If effectively implemented, this procedure would eliminate any potential insights into developmental correlation. However, the complexities of developmental genetics mean that this is not a practical recommendation; many phenotypic characters are demonstrably under highly polygenic control, while single key genes frequently regulate many features of an organism (pleiotropy). The best approach to coding a species for morphological cladistic analysis is to describe as many features as possible that can be delimited and can reasonably be assumed to be under genetic control, leaving developmental correlation to be assessed *a posteriori*.
- 2 Long branches tend to be especially mutually attractive during tree-building, often yielding incorrect topologies (long-branch effects: e.g. Hendy and Penny,

1989); in such cases the long branch will no longer be present to be examined for evidence of saltation, having been substantially shortened in order to insert the long-branch taxon into an incorrect position on the cladogram.

- 3 Even if sampling of known species is maximised, long morphological branches could still reflect at least two non-saltational evolutionary scenarios. First, they could be due to the absence (most commonly by extinction) of several phylogenetically intermediate species. Second, it could conceivably reflect the acquisition of several phenotypic characters by a lineage in the absence of any divergent speciation (i.e. by anagenesis). Although there is limited direct evidence that anagenetic evolution takes place (but see Section 7.7.2), equally it is difficult to demonstrate that the observed character-state transitions accompanied a single speciation event.

7.4 Punctuated equilibria in morphology, plus phyletic gradualism in DNA sequences, equals evolution

That morphological and genetic changes are not always parallel seems entirely reasonable at first, but this statement must be tempered by the fact that establishing the extent of 'great morphological change' is highly subjective. Like 'key' characters, it is likely to be influenced by a single novelty that we view as significant because it epitomises a highly successful group of plants. The importance of such single novelties must be viewed against the backdrop of the majority of traits still shared by all taxa due to overall genetic similarity ... Statements like 'rapid radiations are from first principles better tracked by morphology than molecules' (Bateman, 1999: 432) are based on the assumption that specific novelties are adaptive and successful from the onset. Individual novelties only appear important because we know that particular groups are successful today. At the time when they first evolved, such novelties would not be highly significant because the overall genetic environment would still have been similar to that of their close relatives.

(Chase *et al.*, 2000: 166–167)

The 1990s were also characterised by ongoing debates regarding whether the punctuational pattern of evolution perceived and widely popularised by S. J. Gould, N. Eldredge and others (Eldredge and Gould, 1972; Gould and Lewontin, 1979; Eldredge, 1992; Gould and Eldredge, 1993) was real, rather than an artefact of the absence from the fossil and living records of a myriad of phylogenetically intermediate species ('ghost' species that would reflect non-preservation due to rapid extinction, persistent rarity and/or relatively poor preservation potential). Recent reviews of the completeness of the fossil record strongly suggest that the proportion of animal species that ever existed that are preserved in the fossil record is greater than all but the most optimistic palaeontologists had predicted (Donovan and Paul, 1998); it is less clear whether this statement applies equally well to plants.

The best-documented case studies of morphological evolution in the animal fossil record (e.g. Wray, 1995; Jackson and Cheetham, 1999) give great credibility to the reality of the rectangular, phenogram-like pattern inherent in punctuated equilibrium (Figure 7.2a). Furthermore, review of the recent literature suggests that the

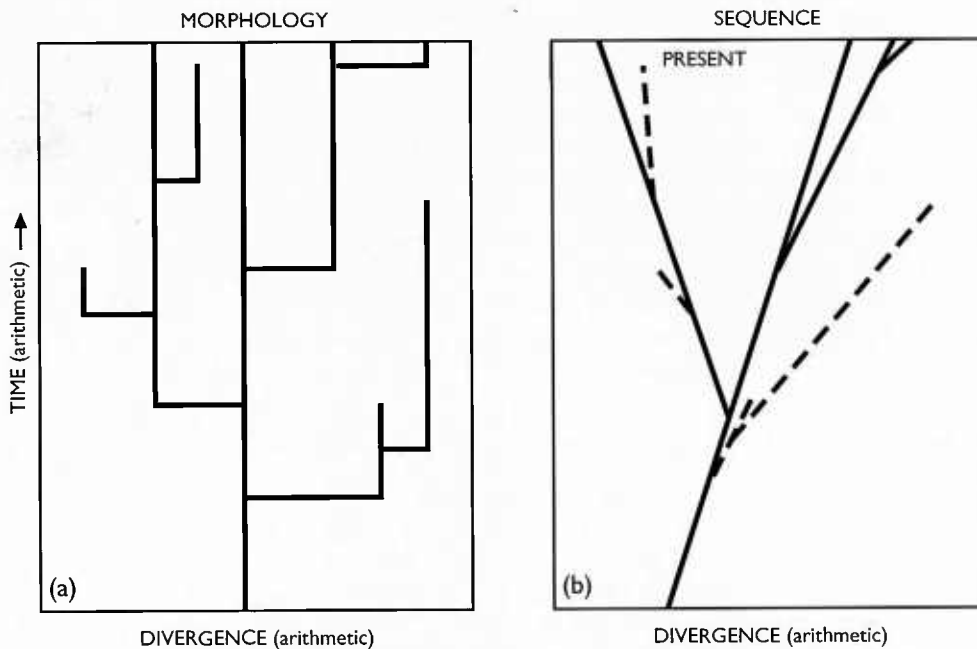


Figure 7.2 A simple hypothetical phylogeny of eight species, four extant and four extinct, all ultimately derived from a single ancestor. Evolutionary patterns are contrasted for morphological data (a), showing geologically instantaneous (punctuational) morphological divergence, and sequences from non-morphogenetic regions of the genome (b), showing constant, clock-like sequence divergence. In this example both speciation events and extinction events are roughly evenly spaced and the magnitude of morphological divergence is random through time; features that maximise the likelihood of correctly reconstructing the phylogeny of the clade (Bateman, 1999a). Note that molecular data cannot determine the relationships of the four extinct species, nor can they separate the most recently divergent of the four extant species from its sister-species (in this example, there has been insufficient time for the novel species to acquire molecular autapomorphies). Also, had the earlier divergences of the three molecularly distinguishable extant lineages been more closely spaced in time (i.e. had they constituted a *bona fide* radiation), we would have been far more likely to satisfactorily resolve their relationships through morphological than through sequence data (modified after Bateman, 1999a, Figure 19.2a, b; see also Bateman, 1996, 1999b).

reality of long periods of evolutionary stasis in specific lineages (i.e. 'equilibrium') is increasingly accepted by both neoDarwinian and supraDarwinian researchers. Bateman (1999a) argued that the most obvious explanation for stasis is that, in most ecological circumstances, neoDarwinian natural selection enhances phenotypic stability. In other words, the background mode of natural selection is stabilising selection, which inhibits evolutionarily meaningful morphological change. The relatively rapid intervening periods of evolution and speciation (i.e. 'punctuation') may occur under the relatively high directional or disruptive selection pressures that underpin neoDarwinian microevolution, or alternatively they may occur even more rapidly under the relatively low selection pressures that are more characteristic of

the various supraDarwinian macroevolutionary scenarios outlined above. In either case, the morphological divergence appears geologically instantaneous.

However, non-fossil phylogenetics was increasingly dominated through the 1990s by DNA sequence phylogenies for regions of the genome that are either non-coding or code for various biochemical pathways that are not morphologically expressed. There are reasons to assume that such regions of the genome have broadly clock-like properties, even if the clock is somewhat unreliable (e.g. Avise, 1994; Sanderson, 1997, 1998). It has become conventional wisdom that, at least in most circumstances, phylogenetically favoured regions of the genome such as plastid genes (Chase and Albert, 1998) and nuclear ribosomal genes (Hershkovitz *et al.*, 1999) accumulate non-lethal mutations with the semi-regularity of a Geiger counter (admittedly, evidence continually accrues of clear contraventions of this 'steady state'). Thus, first principles suggest that these sequence data change by something approaching phyletic gradualism (Figure 7.2b).

Hence, rather than being alternative patterns of evolutionary change that justifiably engender keenly-fought arguments among evolutionary theorists, evolution typically occurs via both punctuated equilibria (morphology) *and* phyletic gradualism (DNA sequences: Figure 7.2). As concluded by Bateman (1999a: 446),

if morphological evolution follows a punctuational pattern (dictated by long periods of stabilising selection that are only occasionally broken by temporary release from selection and consequent speciation) and thus there is no morphological clock, but if in contrast genomic mutation is broadly clock-like, then in phylogenetic terms the vast majority of morphological character-state transitions occur *during* speciation events and the vast majority of molecular character-state transitions occur *between* them.

This important conclusion primarily contrasted morphological phylogenetic data with sequence data for the regions of the plant genome used routinely to infer plant phylogeny, which lack morphological expression. The key morphogenetic genes at the heart of this chapter are also likely to mutate in a broadly clock-like fashion (e.g. Möller and Cronk, 2001) but there the similarity ends. Contrary to the quote from Chase *et al.* (2000) that began this section, there is no requirement for instantaneous, well-honed adaptation, nor for the key gene to wait (at least, not for long) for its cohort of attendant genes to follow its evolutionary lead in order to create a novel 'overall genetic environment'. Genetic control of morphogenesis is not a democracy; rather, key characters reflect key transitions in key genes that are capable of autocratically altering the environment of gene expression.

Before exploring these concepts further, we will present two case studies to illustrate the morphological elements that underpin saltation theory.

7.5 Recognising and interpreting terata in extant and extinct species

[E]veryone admits that there are at least individual differences in species under nature. But, besides such differences, all naturalists have admitted the existence of varieties, which they think sufficiently distinct to be worthy of record in

systematic works. No one can draw any clear distinction between individual differences and slight varieties; or between more plainly marked varieties and subspecies, and species.

(Jones, 1999: 447)

Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected . . . It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names.

(Jones, 1999: 463)

Bateman and DiMichele (1994a) used two detailed examples to illustrate saltation. Reticulate saltation (little discussed in this chapter) was exemplified by the phylogenetic study of the asterid genus *Montanoa* (Funk and Brooks, 1990), which showed multiple origins of polyploids, each intimately related to similar transitions in ecological preferences (like many studies initially investigated by morphological cladistics alone, this interpretation required some revision following the acquisition of sequence data).

Dichotomous saltation (the focus of this chapter, as it is mutationally driven) was illustrated using frequent and profound architectural transitions within the largely fossil clade of rhizomorphic lycopsids (Bateman *et al.*, 1992; Bateman, 1994). Although a dominant element in Palaeozoic floras (Phillips and DiMichele, 1992), this clade has left only a single extant genus, *Isoetes* (including *Stylites*), which is highly morphologically reduced and ecologically specialised. This paucity of extant descendants renders the clade as a whole immune to both molecular phylogenetics and comparative evolutionary–developmental genetics. The arguments in favour of a strong evolutionary–developmental underpinning to the remarkable morphological diversification of the clade were therefore of necessity based on indirect, circumstantial evidence, which leaves the case unproven, however credible the underlying logic and biological inferences.

Here we will briefly review two other case studies that illustrate various aspects of dichotomous saltation: the first is based on a wholly extinct group of Palaeozoic gymnosperms, whereas the second concerns extant terrestrial orchids, particularly those of the subtribe Orchidinae.

7.5.1 Palaeozoic lyginopterid pteridosperms: transient loss of gender segregation

The earliest seed-bearing plants were the lyginopterid pteridosperms, which probably evolved from a single progymnospermous ancestor in the late Devonian (e.g. Rothwell and Scheckler, 1988). The pattern of morphological character acquisition within the group demonstrates progressive increase in reproductive sophistication (Retallack and Dilcher, 1988; Rothwell and Scheckler, 1988), but there is strong circumstantial evidence that even the earliest pteridosperms segregated male reproductive organs (clusters of increasingly synangial pollen-organs producing proximally

germinating pre-pollen) from female reproductive organs (increasingly cupulate clusters of increasingly integumented ovules). The most common architectural model shows strong developmental similarity between male and female architectures; both were borne in dichotomously and three-dimensionally branching structures in the forks of complexly branched pinnate fronds. The most complete known specimen of such a plant, *Diplopteridium holdenii*, bears several fertile fronds, and each frond is uniformly female (Rowe, 1988). Thus, the available evidence strongly suggests that the plants were either dioecious or at best sequentially monoecious, presumably to ensure cross-pollination.

The only known exception to this rule is a single barely hermaphrodite specimen of the early Carboniferous lyginopterid ovulate cupule *Pullaritheca longii* (Long, 1977a, b; Rothwell and Wight, 1989); all other 38 *Pullaritheca* cupules recovered from two small adjacent outcrops in Southeast Scotland are uniformly ovulate (Bateman and Rothwell, 1990). Each cupule ('hemicupule' *sensu* Long, 1977a) is a pendulous bowl 7–10 mm long and 5–8 mm in diameter, consisting of six to twelve fleshy finger-like lobes surrounding a central discoid placenta (Figures 7.3a and 7.4a). The placenta bears twenty to thirty ovules that terminate in a characteristic chambered ('hydropteridalean') pollen-receiving apparatus, formed from the nucellus and well adapted to accommodate wind-borne pre-pollen grains retracted into the chamber via a pollen-drop mechanism (Figure 7.3b; Rothwell and Scheckler, 1988). The ovules expanded and matured into viable seeds only once they had been pollinated, eventually being shed from the cupule; consequently, most of the ovules remaining in the *Pullaritheca* cupules are unexpanded and abortive, presumably because they had not been pollinated (Figures 7.3a and 7.4a).

The exceptional hermaphrodite cupule was described in detail by Long (1977a), prompting him to indulge in a rare venture into biological speculation. Specifically, it allowed Long (1977b) to resurrect with greater conviction his earlier (Long, 1966) cupule–carpel theory, which suggested that angiosperms could have evolved directly from derived Mesozoic pteridosperms such as *Caytonia* (e.g. Harris, 1964; Retallack and Dilcher, 1988) by retention of the ovules within fully fused sterile cupules. This

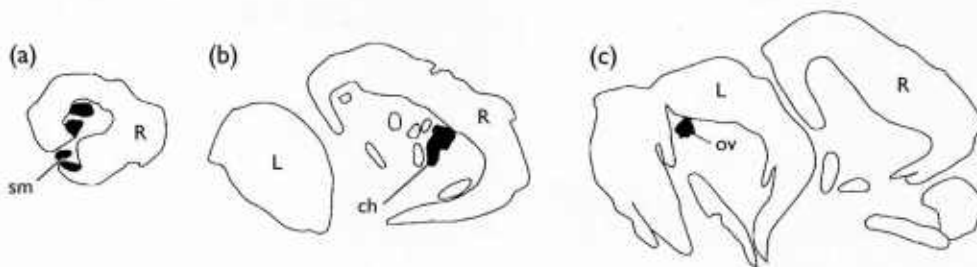


Figure 7.3 An example of a fossil putative teratos from the Lower Carboniferous of Oxroad Bay, East Lothian, Scotland. Longitudinal sections through the margin of an exceptional specimen of the early seed-fern cupule *Pullaritheca longii* (Lyginopteridaceae: Pteridospermales), showing a transition from (c) regulated expression of ovules to (a) atavistic expression of microsporangia via (b) non-functional structures of indeterminate gender. (a–c) modified from Long, 1977a, Figure 1c, e, i). Labels: L, left hemisphere; R, right hemisphere; ov, ovule; sm, microsporangium; ch, chimaeric structure possessing features of both ovule and microsporangium. ($\times 4.8$: after Bateman and DiMichele, 1994b, Figure 9.)

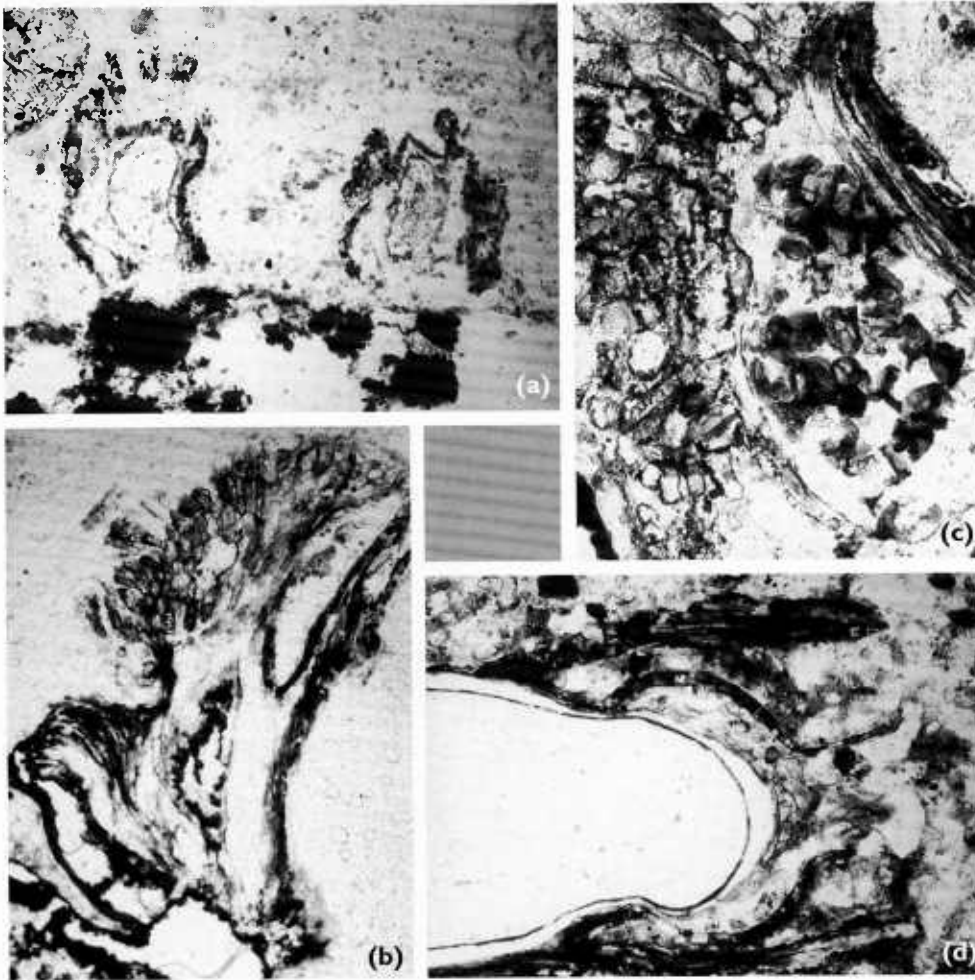


Figure 7.4 An example of a fossil putative teratos from the Lower Carboniferous of Oxroad Bay (see also Figure 7.3). (a) Portion of one of thirty-eight recorded dehiscid specimens of the lobed placental cupule *Pullaritheca longii* that exclusively bear *Hydrasperma longii* ovules, showing retention of a few small abortive ovules attached to the vascularised placenta. (b–c) Two teratological structures first discovered by Long (1977a) at the margin of a single atypical cupule, suggesting ectopic expression of microsporangia; (b) largely resembles an abortive ovule but has undergone exceptional proliferation of the distal nucellar tissue that is normally adapted for capturing pre-pollen grains; (c) shows similar nucellar proliferation to (b), but contains many poorly-formed microspores rather than the expected single permanently retained megaspore. (d) The typical pollen-receiving chamber of *Hydrasperma* ovule, compressed by development of the ovum following successful fertilisation (see also Long, 1977a, b; Rothwell and Wight, 1987; Bateman and Rothwell, 1990; Bateman and DiMichele, 1994b). Magnifications: (a, b, d) $\times 63$, (c) $\times 125$. Photographs by RMB.

theory was dealt an apparently fatal blow by well-known morphological phylogenetic analyses of the 1980s and 1990s (beginning with Crane, 1985; Doyle and Donoghue, 1986). These phylogenies consistently resurrected and promoted the Anthophyte hypothesis, which interpolated between paraphyletic pteridosperms and monophyletic angiosperms various putatively derived gymnosperms (conifers and their relatives, pentoxylaleans, bennettites, and gnetaleans), rendering impossible the direct transition from pteridosperm to angiosperm.

However, this conclusion has been seriously challenged by some arguments that revised morphological homologies place the bennettites as sister to the cycads (W. Crepet, pers. comm. 2001) and, more importantly, recent polygenic phylogenies that placed the gnetophytes as a derived clade within a now monophyletic clade of extant gymnosperms (cf. Mathews and Donoghue, 1999; Qiu *et al.*, 1999; Chaw *et al.*, 2000; Frohlich and Parker, 2000; Graham and Olmstead, 2000). This topology was supported by evolutionary–developmental genetic evidence of synapomorphic loss of the Needle copy of *lfy* from angiosperms (Frohlich, 2001, 2002), prompting the development of the Mostly Male theory of angiosperm origin (Frohlich and Parker, 2000; Frohlich, 2001, 2002), which requires the ectopic expression of ovules on formerly male sporophylls. Does the hermaphrodite *Pullaritheca* cupule have any bearing on the credibility of these important but highly speculative hypotheses?

- 1 The existence of thirty-eight wholly ovulate cupules demonstrates that the one recorded hermaphrodite cupule is an exceptional occurrence that has taken place within a routinely unisexual species (in other words, the hermaphrodite cupule is a developmental ‘accident’), especially when viewed in the context of the fact that all other Palaeozoic pteridosperms have reliably unisexual reproductive clusters.
- 2 The near-radial symmetry of the cupule contrasts strongly with the localisation of the sporangia along a small, marginal portion of the placenta (Long, 1977a) (Figure 7.3). More symmetrical segregation of the genders, most probably with the male sporangia distributed along the entire periphery of the placenta, would be expected from a stable, genetically controlled hermaphrodite cupule.
- 3 The presence of two phenotypically intermediate structures at the junction of the ovulate and microsporangiate zones of the placenta also casts doubt on the stability of the hermaphrodite phenotype. One of these structures (Figure 7.4b) largely resembles the abortive *Hydrasperma* ovules shown in Figure 7.4a, retaining the tentacle-like distal lobes of the integument that give this ovule-genus its name. However, the nucellus-derived pollen chamber (Figure 7.4d) is absent, being replaced by an asymmetric, ‘cancerous’ outgrowth of the nucellus. This nucellar proliferation is also evident in the second structure (Figure 7.4c), which otherwise more closely resembles a microsporangium, even producing within the nucellar envelope a large number of incompletely formed pre-pollen grains.

Taken together, these three observations suggest to us that the developmental anomaly is the product of a local physiological perturbation rather than being genetically determined. The two phenotypically ‘hybrid’ structures imply that there was a breakdown in gender control across the placenta and that the mechanism of gender control was expressed clinally. This accords with gender control of the unisexual

cones of extant conifers, where nutritional clines separate pollen-bearing cones from the better resourced ovulate cones. In the case of the hermaphrodite *Pullaritheca* cupule, one possible explanation lies in the apparently relatively poor vasculature supplying the microsporangium-bearing margin of the cupule (R. Bateman, unpubl. obs.).

Thus, the cupule is undoubtedly a teratos, reflecting an instantaneous phenotypic shift within an individual, but if the above interpretation is correct, it is not a *bona fide* hopeful monster (Table 7.1), as the phenotypic shift is not heritable. Nonetheless, the aberrant cupule provides a useful insight into the control of gender expression in pteridosperms, which in turn suggests that a genuinely genetically controlled mutation could indeed allow ectopic expression of male structures on a fundamentally female structure to produce a flower precursor. It also suggests the feasibility of the converse phenomenon, namely ectopic expression of female structures on a fundamentally male structure, that is required for the Mostly Male theory (Frohlich, 2002). And lastly, it indicates the potential contribution to plant evolution of heterotopy.

Strictly, *heterotopy* is a spatial shift in a developmental programme and its resulting phenotypic structure across the bauplan of an organism (cf. Bateman, 1994; Crane and Kenrick, 1997; Frohlich and Parker, 2000; Baum and Donoghue, 2002; Cronk, 2002; Kellogg, 2002; Rudall and Buzgo, 2002). In the utilitarian terminology of Baum and Donoghue (2002), a shift of a structure to a new location is termed a 'neoheterotopy', whereas the at least partial replacement of a pre-existing structure is a 'homeoheterotopy' (complete replacement of the structure constitutes homeosis *s.s.*: see also the following section).

Given their pivotal position in the phylogeny of seed-plants, it is especially unfortunate that there are no extant pteridosperms available to be subjected to the full panoply of evolutionary–developmental genetic techniques. In order to learn more of the evolutionary power of heterotopy, we will now consider a strongly contrasting clade that has an exceptionally poor fossil record (e.g. Mehl, 1986) but is remarkably species-rich in the extant flora.

7.5.2 Floral symmetry and speciation in orchids: many attempts yield few successes

7.5.2.1 Background and terminology

The literal blossoming of plant evolutionary–developmental genetics was spear-headed by studies of heterotopy *sensu lato* in relatively derived eudicot angiosperms (notably the model genera *Antirrhinum* and *Arabidopsis*), allowing elucidation of the basic ABC model of organ identity (e.g. Coen and Meyerowitz, 1991) that is now becoming far more complex as new data constantly demand revisions and amendments (e.g. Cubas, 2002; Theissen *et al.*, 2002). It was inevitable that this would soon lead to reconsideration of an old evolutionary chestnut, floral symmetry (e.g. Coen, 1999; Endress, 1999, 2001; Cubas *et al.*, 2001; Cubas, 2002; Knapp, 2002; Rudall and Bateman, 2002).

To classical morphologists the traditional primary distinction in floral symmetry separates 'regular' radial symmetry (actinomorphy) from 'irregular' bilateral symmetry

(zygomorphy), though this fundamental dichotomy requires amendment to take into account of irregular flowers that lack any recognisable symmetry (asymmetric *sensu* Endress, 2001; anartiomorphic *sensu* R. Bateman and L. McCook, unpubl. obs.). Actinomorphy and zygomorphy can be defined largely on recognisable numbers of mirror planes (planes that divide the flower into two mirror images when viewed perpendicular to the pedicel); there are at least two and usually more in actinomorphy, and typically one in zygomorphy (a few zygomorphic flowers possessing four mutually perpendicular sepals and/or petals arranged in opposing pairs of unequal size have two unequal mirror planes: Rudall and Bateman, 2002).

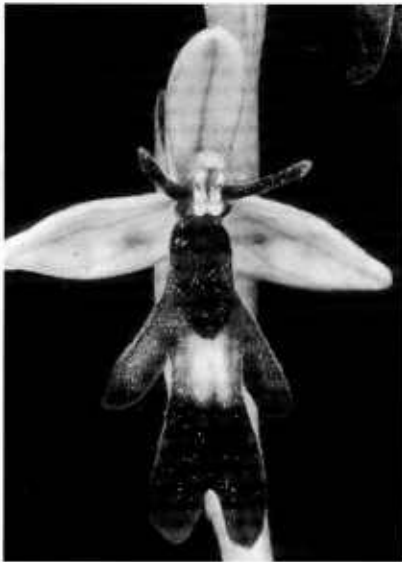
Sadly, this well-established botanical terminology has been mutated by developmental geneticists to create a tension that is clearly evident in this volume; actinomorphic flowers have been termed 'symmetrical' and zygomorphic flowers 'asymmetrical', prompting Endress (1999, 2001) to redescribe actinomorphic flowers as polysymmetrical and zygomorphic flowers as monosymmetrical. Here, we retain the standard botanical terminology, noting also that (a) with regard to the vertical axis in zygomorphic flowers the botanical preference for the term 'dorsiventral' is more linguistically correct than the prevalent developmental genetic preference for the term 'dorsoventral' (cf. Brown, 1956), and (b) the term dorsoventral has a contrasting meaning in the developmental anatomy of animals (Kaplan, 2001a).

A third complication is that these descriptions of symmetry tend to be used to characterise the whole flower, when the symmetries of each of the four fundamental whorls can in theory be different (often, perianth symmetry is prioritised and stamen and carpel symmetry are essentially ignored: Bateman, 1985). For example, the flowers of *Antirrhinum* are zygomorphic in all four whorls, whereas those of *Arabidopsis* appear actinomorphic until one observes the characteristic but subtle bilateralism evident in stamen insertion and early sepal development. It is therefore preferable to consider the symmetry of each of the four whorls separately, rather than attempt to summarise the symmetry of an entire flower in a single aggregate term.

7.5.2.2 A survey of floral terata in terrestrial orchids

Bateman (1985) reviewed occurrences of floral terata among British orchids, focusing on examples of peloria: any transition from zygomorphy to actinomorphy or vice versa (see also Leavitt, 1909; Theißen, 2000). Noting that the gynostemium (a fusion of the male and female whorls) always retained a degree of bilateralism, he focused on transitions in floral symmetry of the three sepals plus the three petals, taking into account the usual strong morphological differentiation of the median petal. This petal, termed the labellum, acts as a landing stage for pollinating insects in most species; hence, although it is developmentally uppermost, in most cases it is spatially lowermost; in erect inflorescences this is due to a 180° torsion of the ovary that is termed 'resupination' (Ernst and Arditti, 1994; Rudall and Bateman, 2002).

Three categories of morphological transition were evident: type A peloria, when the two lateral petals are replaced by two additional labella (cf. Figure 7.5a, b), the less common type B peloria, when the labellum is replaced by an additional lateral petal, and a third category of more heterogeneous morphological transitions that were collectively termed pseudopeloria by Bateman (1985). Here, the modified



(a)



(b)



(c)



(d)

Figure 7.5 Two examples of extant teratos and putative hopeful monsters from the orchid subtribe Orchidinae. (a) is a typical flower of the insect-pollinated orchid *Ophrys insectifera* from Hampshire, England, that shows complex adaptations for transfer of pollinia via cephalic pseudocopulation by male solitary wasps. (b) is a flower of an adjacent individual showing type A perianthic peloria *sensu* Bateman (1985); the two mimicked 'antennae' of (a) have been homeotically replaced by additional 'bodies'. (c) is a typical flower of *Platanthera chlorantha* from Perthshire, Scotland, that shows a long, nectariferous spur, fragrance and white coloration adapted to attract night-flying moths as pollinators. (d) is the flower of an adjacent individual showing pseudopeloria *sensu* Bateman (1985); the petals of the normal flower, including the elaborate labellum and spur, have been replaced by three additional sepal-like structures (see also Figure 10 of Rudall and Bateman, 2002). Magnifications: (a) $\times 2.5$, (b) $\times 1.9$, (c) $\times 2.9$, (d) $\times 2.6$. (a–c) by RMB, (d) courtesy of R. Bush.

labellum becomes less distinctive than the typical labellum but can still be differentiated from the lateral petals and so confers a degree of zygomorphy to the petal whorl (cf. Figure 7.5c, d; Plate 1a, b). Often, the modified labellum more closely resembles the sepals than either the lateral petals or the normal labellum, and hence it is frequently termed 'sepaloid' in the literature. Similar floral transitions occur in other plant families but are rarely described, perhaps because they are less immediately obvious than genuinely peloric morphs. Adding a fourth (and rarer) phenomenon to the classification of Bateman, Horsman (1990) recognised type C peloria, wherein all three petals are apparently replaced by sepals, generating two near-identical whorls of three perianth segments (see also Lang, 2001).

Given the above definitions, one might interpret both type A and type B peloria in orchids as lateral homeoheterotopy (i.e. a change of organ identity confined to a single whorl, namely the three petals) and type C peloria and pseudopeloria as vertical homeoheterotopy (a change of organ identity between two whorls; in this case, apparent expression of three sepals and one sepal respectively in the relatively acropetal petal whorl). However, in most cases of pseudopeloria it is also possible to view the 'sepaloid' labellum as reflecting one or more changes in the timing of development (*heterochrony*); specifically, its simplicity relative to the typical labellum could in theory reflect a labellum whose development had either slowed (neotenic) or ceased abnormally early (progenetic) to yield a mature structure that resembles the juvenile stage of the homologous structure in a notional ancestral organism (paedomorphic: all terminology pertaining to heterochrony follows Alberch *et al.*, 1979; see also McKinney and McNamara, 1991; Zelditch and Fink, 1996).

Systematic and causal interpretation of such terata depends strongly on the level of comparison of the 'homeotic' (*s.l.*) morph with the normal 'wild type' morph. In the most obvious case, bimodal variation in floral symmetry within a single individual (e.g. Darwin, 1859; analogous to the hermaphroditic *Pullaritheca* cupule described above) is likely to reflect a non-genetic cause or a somatic mutation, and thus be of no evolutionary potential. Nonetheless, interpretation is simplified by the fact that the conspecificity of both morphs is assured, and the identity of the abnormal morph can therefore be determined by comparison with other conspecific individuals bearing only one floral morph. Examples occur widely within the orchid family; the most common manifestation is the duplication of the labellum to produce a perianth of seven segments, a phenomenon that typically affects only the lowermost or the uppermost flowers of a (usually unbranched) orchid inflorescence.

Determining the conspecificity of the homeotic and normal floral morphs becomes more challenging when they are borne on separate individuals. In most cases, both morphs co-exist in a single local population, and resemble each other in all other phenotypic characters. However, distinguishing the normal morph from the homeotic morph (i.e. determining the polarity of the morphological transition) can be challenging, usually relying on the homeotic morph being appreciably less frequent than the normal morph in the populations within which it occurs or, even less convincingly, in its absence from other closely related species. This was the case with the type A peloric individual of *Ophrys insectifera* shown in Figure 7.5b, which was the only such morph observed in an estimated population of 6,000 flowering plants. However, this assumption of relative rarity is not always justified, especially in populations of orchid species that are autogamous; for example, *Epipactis phyllanthes* var.

phyllanthes (Young, 1952; Bateman, 1985) often forms uniformly pseudopeloric populations, presumably because their self-pollination leads to very low genetic diversity (Hollingsworth *et al.*, *subm.*). Under such circumstances, arguments for transitional polarity generally rely on the existence of many populations that wholly lack the putatively homeotic morph (as is the case for *E. phyllanthes s.l.*: Young, 1952). In such cases, the homeotic morph is likely to reflect a mutation (or combination of mutations) that is by definition polymorphic within the populations under scrutiny.

More usefully, previous unsubstantiated assertions of conspecificity or lack of conspecificity between the two contrasting floral morphs can now be readily tested using molecular markers. For example, a wide range of markers failed to detect any differences between normal and pseudopeloric *E. phyllanthes* (P. Hollingsworth, R. Bateman *et al.*, unpubl. obs.). Molecular data are especially valuable for refuting previous accusations of hybrid origins for homeotic (especially pseudopeloric) morphs. McKean (1982) interpreted the orchid shown in Figure 7.5d as a bigeneric hybrid between *Platanthera chlorantha* and *Pseudorchis albida*, whereas Bateman (1985) argued that it was probably a pseudopeloric morph of *P. chlorantha* (Figure 7.5c). This species is frequent at the locality yielding the supposed hybrid, where the vegetation includes several teratologies that are thought to reflect the high heavy metal content of the underlying spoil heaps. Nuclear rDNA (ITS) sequences revealed a large phylogenetic disparity between *Platanthera* and *Pseudorchis* (Bateman *et al.*, 1997; Pridgeon *et al.*, 1997; Bateman, 1999a, 2001) and further studies using molecular markers have conclusively demonstrated that the contrasting plants shown in Figure 7.5c and d are, in fact, both assignable to *P. chlorantha*.

Homeosis becomes of greatest interest to systematists when the putative homeotic morph regularly forms fairly uniform populations and hence becomes recognised as a distinct taxonomic species (cf. Bateman and DiMichele, 1994a; Rudall and Bateman, 2002). In other words, the teratology in question definitely reflects mutation, and that mutation has become fixed in the populations in question. Under these circumstances, we can usefully apply the full panoply of morphological and molecular phylogenetic techniques to the problem.

In some such cases the mutant orchid species is assigned to a pre-existing genus, a good example being the type B peloric cyprapedioid *Phragmipedium lindenii* (e.g. Pridgeon *et al.*, 1999). In other cases, particularly in the Orient, the florally simplified mutant has been controversially recognised not only as a distinct species but also as a monotypic genus that is assumed to be phylogenetically primitive. Of these supposed genera (most of which are lower epidendroids: for reviews see Chen, 1982; Rudall and Bateman, 2002), *Tangtsinia* closely resembles *Cephalanthera*, *Sinorchis* appears attributable to either *Cephalanthera* or, more likely, *Aphyllorchis*, and *Diplandrorchis* and the polyspecific *Archineottia* resemble *Neottia*. Within the orchidoids, *Aceratorchis* is a more widely distributed *bona fide* species that resembles the co-occurring genus *Galearis*. Rudall and Bateman (2002) suggested that, far from being primitive, DNA sequence data will demonstrate that these 'genera' are nested within other more species-rich genera that possess much more strongly differentiated labella. Available data are insufficient to determine whether the morphs show types B or C peloria or pseudopeloria.

A similar example is evident among South African orchidoids of the *Satyrium* group, where two 'subactinomorphic' (pseudopeloric) species possessing reduced

labella and elongate gynostemium have been assigned to the genus *Pachites*. It is not clear whether these two species are sisters, nor whether they are the sister group, and potentially ancestral to, *Satyrium* s.s. or nested within *Satyrium* as secondarily reduced morphs (Linder and Kurzweil, 1999). Although molecular phylogenies have begun to be constructed for South African orchids (Douzery *et al.*, 1999; Bateman *et al.*, *subm.*), this putative genus has not yet been sequenced.

7.5.2.3 Possible post-saltational radiations

In yet other cases, the prospectus not only successfully establishes a new taxonomic species and genus but also subsequently radiates to generate several descendant species, often via polyploidy and/or a transition from allogamy to autogamy. The type B or C peloric genus from Australasia, *Thelymitra*, has been demonstrated using sequence data to be monophyletic (Kores *et al.*, 2001) and contains *c.* fifty species, many of which are autogamous (Bower, 2001; Bateman and Rudall, 2002).

Here, however, we have chosen to focus on the pseudopeloric European genus *Nigritella*, as we have access to both molecular and morphological phylogenetic data and so can conduct a cross-matrix comparison (Figure 7.6: cf. Bateman, 1999a). *Nigritella* contains about fifteen species, most reflecting relatively recent polyploidy events and/or transitions from allogamy to autogamy (Hedrén *et al.*, 2000). ITS sequence data (Figure 7.6b) imply that *Nigritella* is nested phylogenetically within a paraphyletic *Gymnadenia* s.s. (consequently, *Nigritella* was sunk into *Gymnadenia* by Bateman *et al.*, 1997), and that both putative genera are appreciably divergent from their sister genus, *Dactylorhiza*. The morphological cladistic analysis (Figure 7.6a) similarly suggests that *Nigritella* is nested within *Gymnadenia*, but identifies a contrasting sister-species. More interestingly, it also reveals that the equal longest morphological branch in the tree separates *Gymnadenia* s.s. from *Nigritella*. Although the two putative genera are very similar vegetatively, *Gymnadenia* s.s. has far more strongly zygomorphic and fully resupinate flowers that possess long nectariferous spurs and are pollinated by lepidoptera (Figure 7.7a–c). In contrast, *Nigritella* lacks resupination and has only a simplified labellum and vestigial spur (Figure 7.7d–f); these are classic characteristics of pseudopeloria (Bateman *et al.*, 1997, *subm.*; Pridgeon *et al.*, 1997; Bateman, 1999a, 2001; Rudall and Bateman, 2002).

Interestingly, there is no measurable sequence divergence or qualitative morphological divergence among the several (arguably over-split) species of *Nigritella*, prompting Bateman (1999a) to suggest that the radiation of this group, which is confined to alpine and boreal habitats in Europe, may reflect a species-level radiation that occurred since the Pleistocene ice retreated at the close of the Loch Lomond Stadial (Younger Dryas), about 10,000 years ago. However, as noted by M. Frohlich (*pers. comm.* 2001), the present distributions could be the relicts of a genus that was more widespread during the Pleistocene glacials, when terrains suitable for the plants would have been more extensive. In either case, much of the driving force for that radiation appears to have been polyploidy and at least one transition to autogamy, suggesting that the clade is 'attempting' to maximise its fitness within the 'undesirable' constraint of a floral morphology that can no longer support the ancestral lepidopteran pollination syndrome. It is regrettable that greater progress has not been made in the evolutionary–developmental genetics of

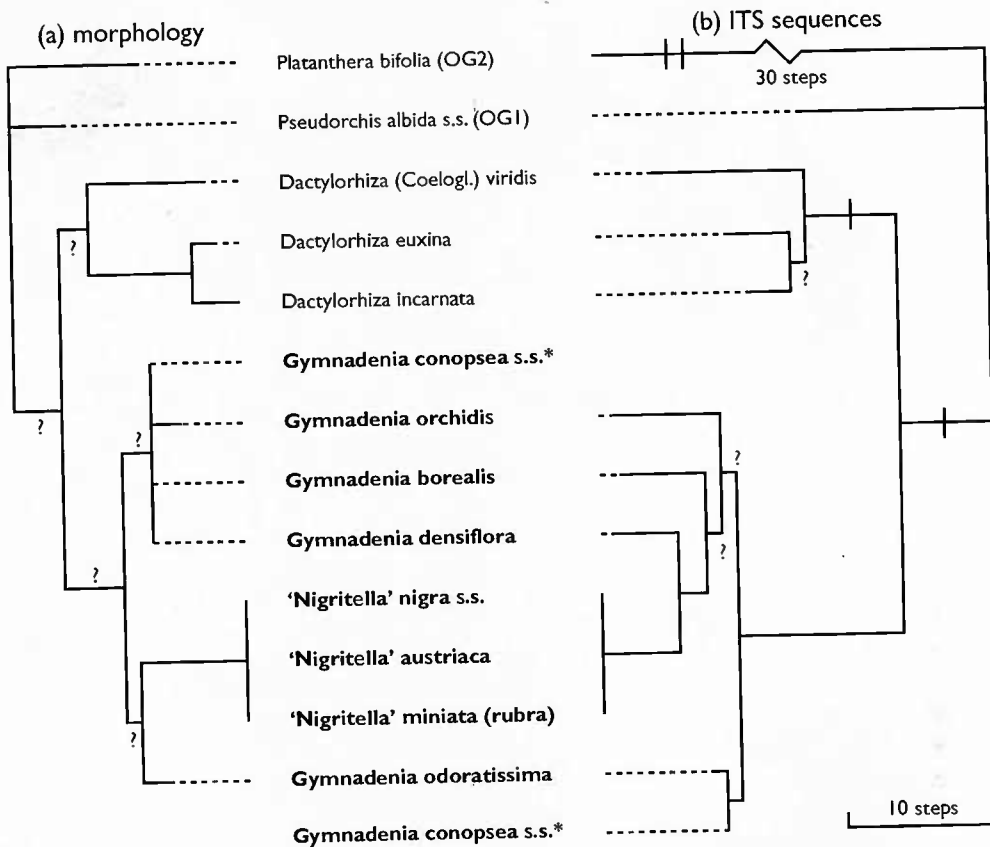


Figure 7.6 Comparison of one of two most-parsimonious cladograms for morphology (a) and one of several most-parsimonious cladograms for ITS sequences (b) for the *Gymnadenia* alliance (boldface), its sister-group the *Dactylorhiza* alliance, and *Pseudorchis* plus *Platanthera* as a paraphyletic outgroup (all Orchidinae: Orchidaceae). Branch lengths are proportional to the number of steps under Acctran optimisation. Cross-bars indicate unambiguous indels; nodes bearing question marks have less than 80 per cent bootstrap support. Note the incongruent positions between the two trees of *Gymnadenia conopsea* s.s. (asterisked). (a) from R. M. Bateman, I. Denholm and P. M. Hollingsworth (unpubl. obs.), (b) from R. M. Bateman, P. M. Hollingsworth and J. Preston (unpubl. obs.).

orchids (for summary see Johansen and Frederiksen, 2002), as we suspect that a single mutation in a key developmental gene triggered the origin of *Nigritella* from within a species of *Gymnadenia*, stochastically forcing subsequent evolution in the lineage along a very different path from the plant-pollinator co-evolution that had previously driven evolution in the lineage.

7.5.2.4 Radiation of the orchid family

Reviewing the origin and initial radiation of the orchid family, Rudall and Bateman (2002) noted the importance of heterochrony, heterotopy, organ suppression and



Figure 7.7 A putative example of a homeotic transformation leading to the immediate origin of a new orchid genus, based on the phylogenies depicted in Figure 7.6 which suggest that *Gymnadenia densiflora* (a–c) is the most likely ancestor of the *Nigritella* alliance, here represented by *Nigritella austriaca* (d–f). The two putative genera are very similar vegetatively but differ strongly in floral morphology: compared with *Gymnadenia* s.s., *Nigritella* has a more compact pyramidal inflorescence and non-resupinate flowers bearing a poorly differentiated labellum and a vestigial spur that lacks nectar (a–f from Landwehr, 1977). Magnifications: (a) $\times 0.30$, (b–c) $\times 1.5$, (d) $\times 0.59$, (e–f) $\times 2.1$.

organ fusion in underpinning gross morphological divergence; processes that typically leave the two distal floral whorls of the orchid flower fused and at least the three distal floral whorls bilaterally symmetrical. The origin of the family was probably facilitated by epigyny and the mycorrhizal association that encouraged the maturation of many small seeds per ovary, but strictly is delimited by bilaterally symmetrical suppression of at least half of the six ancestral stamens, with

subsequent multiple reductions to two functional stamens and a single reduction to one stamen (each group possessing at least some species with one or more relictual staminodes, and occasional atavistic reversals to greater numbers of stamens and/or staminodes). Style–stamen fusion formed the gynostemium, and petal–stamen (or possibly petal–staminode) fusion may have formed the labellum. Differentiation of the labellum conferred bilateral symmetry on the whorl of three petals, which is inserted immediately distal to the more equidimensional whorl of three sepals. Finer-scale phylogenetic divergences in floral form tend to involve modifications of the size, shape and colour of the labellum and associated spur (where present).

Within the context of this evolutionary history, Rudall and Bateman described both type A and type B peloria as examples of lateral homeoheterotopy, with median petals (i.e. additional labella) replacing lateral petals and lateral petals replacing median petals, respectively. Both are also genuine examples of homeosis *sensu* Baum and Donoghue (2002), as they show positional translocation during evolution of an entire pre-existing structure. However, pseudopeloria was attributed not to vertical (in this case acropetal) homeoheterotopy (translocation of a sepal to the location normally occupied by the median petal) but to heterochrony; specifically, the median petal remains recognisable (albeit less morphologically distinct). The considerable variation in morphology evident among pseudopeloric individuals indicates that several genes (probably expressed downstream of the better-known homeobox genes) may be involved in such transitions. Pseudopeloria also appears more likely to disrupt the structure of the gynostemium than is peloria, tentatively indicating that separate sets of developmental genes control perianth zygomorphy and gynostemial fusion. These morphologically-based inferences are now amenable to testing using evo-devo techniques.

7.6 Plant versus animal evolution

Plants work to rules rather different from those of animals. They are more ready to accept a foreign mate, and, quite often, the offspring of such a liaison find themselves with combinations of genes that fit together so well that the new mixtures flourish. Hybridisation becomes a fast track to a new existence, rather than (as in animals) a crack through which DNA leaks to dilute the prospects of a hopeful species . . . Plant species can, it seems, originate at some speed, with no need for the long probation in new forms of animal life. Their genes are more ready to cooperate than are those of animals.

(Jones, 1999: 242)

Our 1994 paper included a forthright critique of zoocentrism. The above quote from Jones (1999) is a welcome indication that plants are at last entering into the thinking of some of the most effective popular exponents of evolutionary theory: influential scientists who are inevitably drawn from the zoological or palaeozoological communities. The list of major differences in both the generation and establishment phases of saltation presented by Bateman and DiMichele (1994a; see also Darley, 1990) can now be considerably expanded.

Perhaps the most important factor is the sedentary, autotrophic lifestyle of almost all higher plants and their consequent reliance on a root–shoot dichotomy and on

the multiple localised meristems that allow open, additive growth and differentiation, and offer the potential for clonal vegetative reproduction. The majority of the component organs are, of necessity, ephemeral serial homologues (rootlets, leaves, leaf-derived floral organs of the four angiosperm floral whorls, pollen, ovules), and most of these terminate ontogenetic cascades, minimising the ontogenetic constraints inherent in the concept of 'burden' (Riedl, 1979) and maximising the potential for evolutionary mosaicism (Stebbins, 1983).

The history of green plants since their single putatively Silurian invasion of the land (Kenrick and Crane, 1997; Bateman *et al.*, 1998) owes much to diversification in the type, number, spatial arrangement and branching patterns of meristems, which along with dormancy substitute for the motility of animals (Darley, 1990). Moreover, the largely 'on-off' nature of meristematic control, and the inability of plant cells to translocate within the plant body once the cellulose cell wall has formed, reduce the potential for gradual transitions in form, either within specific organs or between adjacent organs.

Also, there is no juvenile sequestering of gametes in plants; any meristem can in theory undergo mutations that are subsequently passed on to meiotically-derived sets of 'sibling' gametes generated during the next reproductive phase of the plant. The regularly repeated phases of reproduction that characterise most plant life cycles also provide far greater opportunities for polyploidy, arguably enhanced by self-generated chemical spindle inhibitors and externally imposed physical shocks (Cronk, 2001); moreover, there is increasingly strong evidence that mutant embryos are far less frequently aborted in plants than animals.

7.7 Establishing hopeful monsters

[E]ach new species is formed by having had some advantage in the struggle for life over other and preceding forms. From the extraordinary manner in which European productions have recently spread over New Zealand we may believe that in the course of time a multitude of British forms would exterminate many of the natives. Under this point of view, the productions of Great Britain may be said to be higher than those of New Zealand. Yet the most skilful naturalist, from an examination of the species of the two countries, could not have foreseen this result.

(Darwin, 1859; rewritten by Jones, 1999: 303)

Evolution's progress (if such it is) is not uninterrupted. Catastrophe on a scale unknown to history has played a part. Whether it had a constructive, rather than a merely lethal, effect is another issue. Some claim that mass destruction led to biological explosions as the survivors evolved to fill the gaps. If they are right, cataclysms drive change as much as does slow modification.

(Jones, 1999: 292)

We argue in the following section that the field observations of many generations of natural historians (such as those discussed for the Orchidaceae in Section 7.5.2), now supported by detailed studies of model plants (e.g. Meyerowitz and Somerville, 1994) and causal explanations recently provided by various subdisciplines of

molecular biology, constitute an irrefutable case for the widespread occurrence of macromutations. However, these are not Goldschmidt's concept of genetically extensive mutations, but rather are typically very small genomic changes of large phenotypic effect. Thus, we believe that future conceptual battles over the credibility of saltation theory are far more likely to be fought over the viability of the prospectives in natural habitats (Bateman and DiMichele, 1994a, b; DiMichele and Bateman, 1996; Bateman, 1999a) than over previous erroneous scepticism regarding whether macromutation occurs. Sadly, the profound advances in developmental genetic knowledge achieved since 1994 that have helped to conclusively demonstrate the ubiquity of macromutation (see below) have not been matched by corresponding new insights into the all-important ecological filtration of novel phenotypes. Nonetheless, we will now review (and, where appropriate, amend) our previous scenario.

7.7.1 The model: ecological filtration in primarily and secondarily vacant niches

Once it has originated as a single mutant or small colony of sibling mutants, the prospectives must be sufficiently functional to establish itself within its local environment and subsequently to reproduce (though note that there are several alternatives to sexual reproduction available to plants; initial sterility is not necessarily a bar to successful establishment). Considerable expansion in the size and range of the population is then required to protect the now fully-fledged taxonomic species from the vicissitudes of the environment and from competition (albeit indirect, environmentally-mediated competition for resources) with other plant species, not least the parental species (Bateman and DiMichele, 1994a, b; DiMichele and Bateman, 1996).

In our previous models we assumed lower fitness of the hopeful monster than its parents and hence emphasised (possibly over-emphasised) the benefit of the prospectives originating serendipitously in a habitat of low competition that allows at least temporary respite from selection pressures. In this context, there exists a strong contrast between examples of relatively low infra- and interspecific competition associated with (a) the initial invasion of a previously unoccupied habitat type by plants following their invasion of the land (Bateman *et al.*, 1998) and (b) establishment in habitats that have become temporarily vacant over a specific geographical area due to one or more major environmental perturbations.

The greening of the terrestrial realm during the Palaeozoic is essentially a story of diversification into increasingly stressful (especially increasingly xeric) environments (Bateman *et al.*, 1998; Stein, 1998; Kenrick, 2002; Schneider *et al.*, 2002). Each successive phase involved radiations of one or more major taxa possessing a recognisable range of morphologies well adapted to the range of environments being colonised. Major morphological innovations tended to occur at the cutting edge of this wave of colonisation, with consolidation and specialisation characterising previously colonised habitat types (e.g. of lycopsids and sphenopsids in Devonian-Carboniferous wetlands). Reverse colonisations, such as the post-Carboniferous invasion of previously marginal, xeromorphic conifers into the (by then relatively desiccated) adjacent wetlands, were possible only in the wake of severe environmental

perturbations such as the equatorial warming and drying of the Early Permian (DiMichele and Aronson, 1992; Foote, 1996; DiMichele *et al.*, 2001; DiMichele, *subm.*).

Cases involving the occupation of 'secondary' vacancies inevitably dominate the post-Palaeozoic history of the terrestrial flora (e.g. Wing and Boucher, 1998). Here, the identity of the re-occupying species is strongly influenced by three factors. If by good fortune the occupier grew adjacent to, but was unaffected by, the environmental perturbation, its expansion is caused purely by happenstance. If the occupier experienced the perturbation but survived there is ample scope for an adaptive explanation (e.g. fire-induced seed germination in species regularly affected by wild-fires). However, where the environmental catastrophe is insufficiently frequent to be able to influence microevolution, the persistence of the occupier and its subsequent expansion in numbers can only reflect pre-existing properties of the organism; in other words, its success can be attributed to pre-adaptation.

More controversially, Bateman and DiMichele (1994a) also argued that in all these cases the successful invader then benefits from incumbent advantage, a theory that essentially states that mere physical occupancy of a particular site confers an advantage beyond that attributable to raw estimates of intrinsic fitness (e.g. Rosenzweig and McCord, 1991; DiMichele and Bateman, 1996). We further hypothesised that, because of the lack of direct Malthusian competition among individual plants, a much wider range of features of a typical higher plant are selectively neutral at any particular moment in time than are those of a typical higher animal, giving plants considerably more freedom for non-selective experimentation in form (see also van Steenis, 1976).

7.7.2 Relevance of phylogenetic patterns

Thus far, our 'armchair' test of this scenario has been weak and indirect. Specifically, we predicted that the overall pattern of plant morphological diversification through time would appear fractal, with the greatest phenotypic divergences between ancestral and descendant species characterising the earliest lineages in a clade and the least divergences characterising the most recent (DiMichele and Bateman, 1996; Bateman, 1999a, b; DiMichele *et al.*, 2001; see also Arthur, 1984, 2000). In the few clades where strong data sets for both sequences and morphology are available, this does indeed appear to be the case (Bateman, 1999a). There are at least three possible explanations for such a pattern: increased developmental canalisation, increased niche saturation (both resulting from speciation) and preferential extinction of early-formed lineages (the antithesis of speciation).

Increased developmental integration and canalisation through time appear likely from first principles. It is becoming evident that most genes of profound phenotypic effect in higher plants have putative homologues in prokaryotes and early eukaryotes. The subsequent evolutionary history of plant form owes much to gene duplication events (including those engendered by polyploidy) followed by divergence of function of the paralogues, the increase in overall numbers of functional genes presumably being balanced to some degree by 'extinction' of specific genes deactivated through gene silencing or pseudogene formation via events such as transposon insertion (e.g. Wessler *et al.*, 1995; Federoff, 2000; Walbot, 2002). The resulting

enhanced complexity of the developmental control mechanisms is likely to increase the interdependency among specific genes. However, there are two opposing interpretations of the consequences of such interdependency; either the ever-more complex system of sequentially acting genes will become more prone to lethal collapse when faced with a strongly expressed mutation (thereby inducing progressive canalisation), or the probable proliferation of alternative systems, resulting in enhanced developmental homeostasis that can buffer the organism *against* lethal collapse (in which case canalisation is likely to prove to be a largely mythical phenomenon). This issue deserves more attention than it currently receives.

Transferring our emphasis from the generation phase to the establishment phase of saltation, an increased probability of niche saturation inevitably accompanied the well-documented progressive increase in species-level plant diversity through time (e.g. Valentine, 1980; Behrensmeyer *et al.*, 1992). As niche saturation is approached, competition for resources increases and the chances of a novel prospecies finding a low-competition niche in which to establish itself decrease correspondingly. In other words, the rate of generation of prospecies may remain high, but the more critical rate of successful establishment of those prospecies will on average decrease through time. To some extent, this effect may be mitigated by finer niche partitioning of specific habitats; Tertiary angiosperms in particular appear to have benefited from unusually strong co-evolutionary drivers for speciation. However, this exceptional species richness reflects typically trivial morphological differences among species, and is not mirrored in greater diversification of form at higher taxonomic levels (DiMichele *et al.*, 2001).

This observation does raise the thorny issue of whether selective extinction among major clades strongly affects perceptions of patterns of morphological divergence in land-plant phylogenies. It is abundantly clear that the survival of major class- and ordinal-level taxa (both monophyletic and paraphyletic) of pre-angiosperm radiations has been highly selective, with the most profound and troublesome gaps in the extant flora reflecting Siluro-Devonian pteridophytes (e.g. Rhyniopsida, Zosterophylloids, Trimerophytoids, Progymnospermopsida) and Late Palaeozoic–Early Mesozoic seed-plants (e.g. Cordaitales, Pteridospermales, Bennettitales, most Ginkgoales). These gaps can, to some extent, be plugged by fossil taxa in morphological phylogenies, but they seriously undermine attempts to generate molecular phylogenies of land-plants suitable for testing saltation hypotheses. Exceptional sampling of many genes cannot compensate for poor sampling of taxa, and the current trend to eschew morphological phylogenies in favour of sequence data is becoming an increasingly severe handicap to making genuine progress in the understanding of major morphological transitions (cf. Bateman, 1999a; Hawkins, 2002).

Thus, in practice, the best opportunities for empirically testing saltation theory lie among extant angiosperms, tackling sets of closely related species that show recent origins, as inferred from short terminal branches on sequence trees, but considerable morphological divergence, as inferred from long terminal branches on morphological trees (Bateman, 1999a). Good 'mainland' examples occur in Orchidaceae (Bateman, 1999a), Zingiberaceae (Harris *et al.*, 2000) and Fabaceae (Richardson *et al.*, 2001a). Putative evolutionary radiations on geographic and physiographic islands have in recent years provided many such case studies of massive morphological divergence, imposing legendary status on groups such as the Hawaiian silverswords (Baldwin *et al.*, 1998), Macaronesian Poteriaceae (Bateman, 1999a; Helfgott

et al., 2000) and South Atlantic Rhamnaceae (Richardson *et al.*, 2001b), but what has been lacking is the null hypothesis of equally careful studies of groups that have *failed* to radiate.

For example, the twelve orchid species currently recognised in Macaronesia represent eleven genera, and each species has a close analogue in the adjacent regions of the Mediterranean, apparently reflecting anagenetic speciation (R. Bateman, unpubl. obs.). Indeed, the majority of immigrants to oceanic islands over volcanic hot-spots have failed to dichotomously speciate, let alone radiate, suggesting that fresh terrain and low competition is a prerequisite for, rather than a driver of, radical innovation in form. In the case of the Macaronesian orchids, the potential for radiation is constrained not only by the need for fidelity from associated pollinating insects but also apparently from at least two cohorts of mycorrhizal fungi; the first is essential to initiate germination of the minute embryos in the air-borne seeds and the second is needed to supply nutrition to the mature tubers or rhizomes.

7.7.3 Urgent need for field data

The main problem with assessing the establishment phase of saltation (and indeed with demonstrating any evolutionary hypothesis among higher plants) is demonstrating the potential for speciation by making direct field observations. This challenge has been to a large degree abrogated by neoDarwinian theorists on the grounds that the period of time required for speciation via microevolution is too long for observation to be feasible. Also, most supposed cases of microevolution (including the much-vaunted textbook example of the melanic form of the moth *Biston betularia*) do not ultimately lead to speciation, but rather diminish once the directional selection pressure proves transient and subsides or are introgressed back into the fold by the 'parental' populations. By contrast, in the case of saltation, the observer can easily demonstrate the origin (often multiple origins) of a particular morph, as in the orchid floral examples discussed in Section 7.5.2, and by deploying modern evo-devo techniques can (albeit with much effort) identify the causal mutation. Rather, what is lacking is a concerted effort to monitor such lineages in the field in the hope of identifying one of the rare examples of successful establishment.

A few empirical projects have been pursued in experimental plots, most notably the intriguing effects of epidermal cell mutation on pollinator choice in snapdragon flowers discussed by Glover and Martin (2002). However, in these cases the mutation under scrutiny is usually too phenotypically subtle and hence questionably constitutes a *bona fide* macromutation (indeed, most fail to attract the attention of evo-devo researchers at all). Moreover, the massed individuals carefully planted in serried ranks do not experience the environmentally-induced traumas or the challenging cut-and-thrust of interspecific competition that occur in natural ecosystems.

One possible source of stronger field data comes from the sudden intense interest among environmentalists in determining the behaviour of transgenic crop plants in natural and semi-natural ecosystems, which has emerged in the wake of the recent GM controversies (cf. Ellstrand *et al.*, 1999). Detailed monitoring of the possible spread of transgenes from the intended 'host' to other individuals, of both that and other species growing in the habitat under scrutiny, should give greater insights into the integration and dissemination of specific genetic novelties.

7.8 Generating hopeful monsters

However Darwinians may protest (and they do), millions of generations of inertia scarcely fit his image of life as poised for an instant response to any challenge. The argument between supporters of evolution as unhurried Victorian progress and those who hold the modern view of history as boredom mitigated by panic is unresolved.

(Jones, 1999: 294)

7.8.1 A rapidly expanding body of data guided by phylogenies

The examples of teratology discussed in Section 7.5 emphasise the value of the distinction between the general concept of a sudden morphological shift between parent and offspring (of whatever cause) inherent in terata and the narrower concept of a heritable shift reflecting a mutation or epimutation that defines a prospectus ('hopeful monster'). Our 1994 discussion of the generation of hopeful monsters centred on homeotic (notably Hox and MADS-box) genes and their relatives, and a survey of the current volume will demonstrate that this remains the focus of evolutionary–developmental genetics. Nonetheless, the range of genes receiving detailed attention is progressively broadening.

At that time the empirical evidence for the genetic underpinnings of such transitions lay in organisms that were undesirably morphologically simple. Studies of higher plants primarily concerned *Arabidopsis* and *Antirrhinum*, with floral morphogenesis perhaps better understood than vegetative morphogenesis (cf. Poethig, 1990; Coen and Meyerowitz, 1991). Although thale-cress and snapdragon flowers remain at the forefront of plant developmental genetics, much progress has been made on all fronts, and the range of model organisms is now rapidly diversifying. In addition, the crucial choice of such organisms is being carefully guided by increasingly robust phylogenies (e.g. Angiosperm Phylogeny Group, 1998; Pryer *et al.*, 2000). Perhaps the greatest remaining gap in sampling of extant green plants lies in the vast panoply of cryptogamic plants. Studies in progress of model moss *Physcomitrella* and model fern *Ceratopteris* will no doubt yield many new insights (Cronk, 2000), though a study of a long-extinct Devonian rhyniophyte such as *Aglaophyton*, with its near-isomorphic sporophyte and gametophyte generations, would have provided a fascinating exploration of the importance of buffering of gene expression in diploid relative to haploid (Kenrick, 1994; Bateman, 1996).

We do not deny that the view, long-held by virtually all evolutionary biologists, that almost all hopeful monsters are in practice hopeless is correct; such mutations are either physiologically lethal or structurally highly dysfunctional. However, it is also clear from case-studies such as the orchid terata described above (Rudall and Bateman, 2002) that the production rate of profound morphological mutations capable of at least transient existence in natural habitats is extremely high. Rare successful establishment of such mutants is arguably sufficient to explain much of evolution, just as rare fixation of mutant alleles in neoDarwinian populations arguably suffices. Moreover, it is also clear that indistinguishable morphological variants can be generated frequently and repeatedly within a single 'parental' species. Many different mechanisms of mutation and epimutation are now recognised. Also, the

decreasing number of key developmental genes now thought to exist in plant genomes as single copies offers more opportunities for divergence of function (e.g. Cronk, 2002). Thus, there are no guarantees that these multiple origins of similar morphs are genuinely homologous at the molecular level; indeed, it seems likely that there are multiple routes to engendering most profound morphological transitions (cf. Hawkins, 2002). Such causal diversity can only enhance the probability of successful establishment of the prospecies.

Nonetheless, constraints on potential saltational transitions are also evident. Some of the most interesting potential saltations that occur frequently in the land-plant phylogeny involve radical changes in life history or ecological preference, such as terrestrial to aquatic existence (e.g. Bateman, 1996), homospority to heterospority (Bateman and DiMichele, 1994b), autotrophy to mycoheterotrophy (e.g. Nickrent *et al.*, 1998) and allogamy to autogamy (e.g. Hollingsworth *et al.*, *subm.*). We have not encountered in the phylogenetic literature any unequivocal examples of successful reversals of these transitions. It seems likely that, after a very brief period of time, the genetic framework necessary for producing terrestrial adaptations, or hermaphroditic gametophytes, or photosynthesis, or effective incompatibility mechanisms, or reliable relationships with specific pollinators, cannot be resurrected. Indeed, in the case of mycoheterotrophs there is circumstantial evidence of increased mutation rates in physiologically expressed genes *prior* to the transition to mycoheterotrophy, suggesting that the transition may constitute the only remaining evolutionary option for the survival of the affected lineage rather than reflecting the finessed craftsmanship inherent in increased fitness through directional or disruptive selection.

This conclusion offers an insight into the concept of contingency promoted by Gould (1989), who argued that replaying a specific evolutionary radiation, even under similar conditions, would yield dissimilar products. Here, we have demonstrated the iterative origination of very similar floral morphs within single orchid species, and of multiple lineages of mycoheterotrophic orchids. Thus, the real contingency may in fact lie not in the origin of the novel morphology but in the environment in which it originates; it is the post-origination fate of each mutant that is decidedly unpredictable.

7.8.2 Loss of features

One can view the history of plant evolution as one of accumulating an optimal repertoire of phenotypic features underpinned by genetic structures sufficiently rigid to preserve advantageous elements of the phenotype but sufficiently flexible to allow change. The diversity of features and underlying genomes strongly influence both flexibility and complexity.

We have already noted the distinction between the ecological processes that operated during the initial period of land-plant colonisation, when the focus lay in previously unoccupied habitats, and subsequent periods of expansion, when the primary challenge was (and is) locating habitats temporarily vacated by their incumbents. Interestingly, a similar distinction can be drawn between the gradual accumulation of increasingly complex and sophisticated morphological features during the Palaeozoic, and the subsequent challenges of altering form in the face of increased canalisation within lineages and decreased probability of ecological establishment of the

products of macromutation. In such circumstances, re-organising and in many cases eliminating pre-existing phenotypic elements is more likely to lead to radical new body plans (cf. Bateman, 1996; Teotónio and Rose, 2001; Kellogg, 2002). As we noted previously (Bateman and DiMichele, 1994a: 83),

Saltation breaks canalization, toppling the hopeful monster from the adaptive optimum of its parents but also freeing the potential lineage for radical reorganisation of form . . . Superficially, such character losses appear improbable agents for innovative evolutionary change. However, by breaking canalisation and simplifying development, they clear the evolutionary palette for future adaptive innovation. The 'developmental ratchet' (Vermeij, 1987; Levinton, 1988) is reset at a lower level, leaving a combination of adaptation and contingency to define a new evolutionary trajectory for the lineage should it survive the establishment bottleneck.

This statement was followed by several empirical examples of simplification of form revealed by phylogenetic analyses, to which could be added the above discussions of simplification associated with mycoheterotrophy. Some of these examples included discussion of vestigial structures, such as secondary thickening in the aquatic pteridophyte *Isoetes*, that presumably represent unbreakable canalisation. However, as noted by Cronk (2001), the *absence* of a vestigial structure in a putative descendant relative to an ancestor is even more indicative of non-adaptive evolution, since it is more convincingly explained by a sudden catastrophic loss, forcing transfer of function (if any), rather than by gradual diminution in size through micromutation following loss of function. Many examples of changes in number, position, appearance and degrees of fusion among floral organs in angiosperms, such as those outlined for orchids by Rudall and Bateman (2002) and for legumes by Tucker (2000, 2001), are far more parsimoniously explained by outright suppression or duplication of structures through specific mutation or epimutation events small in genetic scale but large in phenotypic effect. This inevitably leads to re-consideration of the potential significance of epigenesis, epistasis, pleiotropy, heterotopy and heterochrony relative to the underlying macromutation(s) – subjects that merit greater discussion than is feasible in this chapter.

7.8.3 Recent advances in core evo-devo data

Which genes are crucial to saltation, how are they modified and how are they expressed? In 1994, no single plant chromosome had been wholly sequenced. At the time of writing (summer 2001), the *Arabidopsis* genome has been sequenced in its entirety (Arabidopsis Genome Initiative, 2000; Walbot, 2000) and several grass genera will soon follow (Adam, 2000). How will these advances aid evolutionary understanding? (cf. Singh and Krimbas, 2000).

Arabidopsis, chosen for its small, compact overall nuclear genome and small number of chromosomes ($n = 5$), has proved to harbour about 120m bases that include 26,000 genes of, at most, 15,000 different kinds, thus resembling in number *Drosophila* and *Caenorhabditis* (Walbot, 2000) and approaching that of *Homo*. The remarkable differences must therefore lie in the precise nature of those genes

(though it is clear that the origins of many of the more important genes preceded the divergence of plants, animals and fungi: Meyerowitz and Somerville, 1994) and their mode of expression. Not surprisingly, the sedentary lifestyle of plants is reflected in their genetic complement; a much higher proportion of plant genes influence cell-wall formation, water and hormonal transport in plants, whereas animals specialise in signal transduction (Walbot, 2000). Plants contain an apparent superfluity of some transcription factors; for example, *Arabidopsis* maintains an order of magnitude more of the still enigmatic MYB transcription factors than does *Homo* (Cronk, 2001). On average, five times as many plant nuclear genes communicate with organellar genomes in plants than in animals or fungi (perhaps not surprising, given that plants uniquely possess plastids), and the much wider range of secondary compounds suggests much more complex biosynthetic pathways (Walbot, 2000) that may be more readily switched among closely related species (Bateman, 1999a).

In terms of pinpointing the genes that underpin evolution, a fascinating cautionary tale was summarised by zoologists Marshall *et al.* (1999), who noted that the high-level Hox gene *Ubx* is able to regulate the fundamental distinction between two-winged and four-winged insects. However, comparison of a two-winged fly with a four-winged butterfly pointed the finger at one or more genes located downstream from the apparently highly conserved *Ubx*. They further noted the demonstration by Averof and Patel (1997) that striking differences in body plan among the major groups of crustaceans primarily reflect the precise location of the initial embryonic expression boundary of *Ubx* and *abd-A*. Also, some intermediate morphologies show reduced levels or mosaic patterns of Hox gene expression, suggesting that morphogenesis may be gradational and reflect gradual accumulation of mutations that modify the degree and location of Hox gene expression. Moreover, during insect evolution, first *Ubx* and then *abd-A* were co-opted to repress limb formation (Palopoli and Patel, 1998).

Many of the contributions to this volume discuss interactions among low copy-number genes of large phenotypic effect. Originally termed 'single-copy' genes, this categorisation has been revised to 'low copy number' genes on the basis of more recent research. Gene duplication, both *en masse* through polyploidy (Walbot, 2000; Wolfe, 2001) and individually, may immediately provide a larger amount of transcript or be followed by a 'gain-of function' mutation. The gain-of-function mutation must occur sufficiently rapidly to prevent loss-of-function mutations from generating a non-expressed pseudogene. The result can be different forms of the same functional protein with subtly different properties, increasing the flexibility of response of the 'host' organism to the environment and potentially resulting in fixed heterozygosity (Cronk, 2001). One great potential benefit of the genomics revolution in general, and comparative whole-genome sequencing in particular, is stronger tests of orthology versus paralogy for these powerful classes of gene.

The most popular examples of interactions among such genes are the interaction of the MADS-IKC genes that lead to the ABC model of floral organogenesis. Comparison of early (e.g. Coen and Meyerowitz, 1991) and more recent (e.g. Kramer and Irish, 1999, 2000; Cubas, 2002; Frohlich, 2002; Gillies *et al.*, 2002; Glover and Martin, 2002; Theißen *et al.*, 2002) accounts of this model show elaborations of the original 'three primary factors generate four whorls' model but no major refutations of the cornerstones of the original hypothesis. The *CYC* and *DICH* genes that

confer zygomorphy on many angiosperm flowers (see discussion of Orchidaceae in Section 7.5.2) apparently represent a relatively recent gene duplication event among TCP/R transcription factors (Cubas *et al.*, 1999; Luo *et al.*, 1999; Cronk, 2001, 2002; Cubas, 2002; Gillies *et al.*, 2002), with *DICH* having a similar function to, but accentuating, *CYC*; moreover, an additional duplication of this gene family has been reported in Gesneriaceae (Citerne *et al.*, 2000). In the vegetative realm, the key meristem-control *KNOTTED*-like genes are divisible into two distinct classes in gene trees (Bharathan *et al.*, 1999), reflecting a pre-bryophyte duplication and suggesting a range of possible interactions between duplicates. Meristematic control by *KNOX*-like genes is down-regulated by *PHAN*-like genes, which are in turn negatively regulated by the *STM*-like genes that ensure that *PHAN* expression is restricted to developing leaves (cf. Harrison *et al.*, 2002; Langdale *et al.*, 2002; McLellan *et al.*, 2002; Tsiantis *et al.*, 2002). And in the antithesis of gene duplication and mutual interaction, the apparent loss of function of one of the two copies of *LFY* during the transition from gymnosperms to angiosperms may have resulted from the transfer of the 'female' function to the still-functional 'male' copy of *LFY*, prompting the origin of the hermaphroditic organisation that characterises most angiosperm flowers (Frohlich and Parker, 2000; Frohlich, 2001, 2002).

Much interesting debate currently surrounds the most likely properties of the genes involved in those morphogenetic cascades that are most pivotal to evolution. Current evidence, though sparse, indicates that genes of a relatively narrow range of expression are less likely to be strongly conserved (and thus evolutionarily recalcitrant) than are those with strongly pleiotropic expression across the bauplan (e.g. Doebley *et al.*, 1997; Doebley and Lukens, 1998) or those that provide the focal point of several biosynthetic pathways (Cronk, 2001). The more focused effects of regulatory genes in general, and transcription factors in particular, make them more probable drivers of evolution, with the emphasis currently on mutations in *cis*-regulatory regions (Marshall *et al.*, 1999; Wang *et al.*, 1999; Cronk, 2001). This view partly reflects the observation that the origin of teosinte from maize involved a selective sweep (rapid incorporation of favourable mutations allowing simultaneous fixation of linked genes irrespective of their contribution to fitness) of the flanking regions of the maize allele of the key developmental gene *TB1*, demonstrating intense selection of the *cis*-regulatory regions but no corresponding selection of the coding region of the gene (Wang *et al.*, 1999). Mutations in control regions that subtly influence spatio-temporal expression patterns are strongly implicated in gain-of-function mutations. One potentially important distinction surprisingly rarely discussed is whether the optimal conditions for success for a typical 'gain-of-function' mutation are substantially different from those needed for a successful 'loss-of-function' mutation.

The relatively few well-founded studies of developmental gene interactions can only have revealed the tip of the iceberg; the gene expression and regulation scenarios surrounding specific morphogenetic transitions will undoubtedly appear more complex with increased knowledge. These are likely to reinforce the distinction made by McLellan *et al.* (2002) between primary genes, whose mutation generates novel morphs, and secondary genes, whose expression patterns are modified as a result of mutations in upstream primary genes. In this context, none of the above discussion covers the genes of modest phenotypic effect that constitute the bulk of

the genes in any particular QTL survey, yet in these genes resides the potential for subtle speciation *without* the simultaneous origination of higher taxa (e.g. the modes of speciation that, for example, allow co-evolutionary switching of partners among closely related orchids). We suspect that these phenotypic transitions – essentially quantitative rather than qualitative in nature – will prove more recalcitrant to causal interpretation than the larger-scale morphological transitions that are the raw materials of saltational evolution. Here, epistatic interactions among genes, often generating multiple component ‘supergenes’, may prove to have considerable explanatory power (papers in Wolf *et al.*, 2000), especially if considered in the context of the epigenetic environment of expression (Jablonka *et al.*, 1992; Jablonka, 1994; Jablonka and Lamb, 1995).

7.9 Integrating the developmental genetics of plants into mainstream evolutionary syntheses

I have now recapitulated the chief facts and considerations which have thoroughly convinced me that species have been modified, during a long course of descent, by the preservation or the natural selection of successive slight favourable variation . . . Why, it may be asked, have all the most eminent living naturalists and geologists rejected this view of the mutability of species? . . .

A few naturalists, endowed with much flexibility of mind, and who have already begun to doubt on the immutability of species, may be influenced by this volume; but I look with confidence to the future, to young and rising naturalists, who will be able to view both sides of the question with impartiality. Whoever is led to believe that species are mutable will do good service by conscientiously expressing his conviction; for only thus can the load of prejudice by which this subject is overwhelmed be removed.

(Darwin, 1859: 480–482; rewritten by Jones, 1999: 459–460)

The above observations lead us to the nub of the (arguably artificial) divide between macromutation and micromutation, namely whether evolutionary transitions reflect modification of many genes of small effect, consistent with neoDarwinism, or modification of very few genes of profound phenotypic effect, consistent with saltation? After reviewing current zoological data, Shubin and Marshall (2000: 324) concluded that ‘it appears that relatively few genetic changes may be responsible for most of the phenotypic differences among species’; thus, initial results appear favourable to saltation theory, but may require reinterpretation.

For example, Marshall *et al.* (1999) reported the work of Doebley and Wang (1997) which demonstrated that the now well-known transition from teosinte to maize originally pursued by Iltis (1983) involved a very small number of genes and was dominated by a single homeotic gene, *TB1* (cf. Kellogg, 2002). They further noted that recent quantitative trait locus (QTL) studies (e.g. Orr, 1998; Goodnight, 2000) among closely related species suggest that major morphological features tend to be controlled by a modest but nonetheless significant number of genes (e.g. the eighteen to seventy-four suggested for leaf shape control, as reviewed by McLellan *et al.*, 2002), results that are superficially intermediate between the predictions of neo-Darwinian (many more) and saltation theory (even fewer). However, this raw figure

disguises an exponential distribution of numbers of genes versus degree of phenotypic effect, with very few genes of large phenotypic effect (indeed, they are of far larger effect than was predicted as viable by Fisher, 1930) and much greater numbers of genes of lesser phenotypic effect (Orr, 1998; McLellan *et al.*, 2002). Marshall *et al.* validly used these observations to criticise the Fisherian concept of evolution being confined to panmictic populations carrying many mutations of small phenotypic effect (Fisher, 1930), and reiterated arguments advanced by Kimura (1983, 1991) that each of the many small mutations is extremely vulnerable to random loss from the population while still very rare (this is, for example, evident from frequent loss of highly adaptive self-incompatibility alleles from angiosperm lineages).

However, Marshall *et al.* then chose to set their insightful observations in the context of neoDarwinian adaptation, in turn criticising Kimura's model on the grounds that it assumed a single step to a new adaptive optimum following a presumed environmental change, rather than a more complex 'adaptive walk' consistent with neoDarwinian models.

There are models that are neither strictly neoDarwinian nor strictly saltational that are consistent with the above observations, falling within our broad category of parasaltation (see Section 7.2.2). The most relevant relate to unusually rapid spread of novel alleles through populations that are small, morphologically and genetically atypical of the 'parental' species, and often allopatric or parapatric: these theories include drift (Barrett and Pannell, 1999), shifting balance (Wright, 1932, 1968; Waddington, 1957; Whitlock *et al.*, 1995; Mallet and Joron, 1999), and crash-flush-founder (Carson and Templeton, 1984; Carson, 1985; Slatkin, 1996), each capable of reforming adaptive gene complexes.

However, many of the data gradually being revealed by both QTL and candidate gene approaches to evo-devo (e.g. Baum, 2002) are most parsimoniously explained by the saltation model of major evolutionary transitions in phenotype. The initial qualitative transition is prompted by mutations that modify or suppress the expression of one or at most very few genes of profound phenotypic effect, conferring instant isolation from its parents; thus, saltation is essentially the sympatric equivalent of the aforementioned parasaltational mechanisms. Then, the resulting radically altered phenotype is gradually honed by natural selection to a phenotype that is subtly better adapted for its environment, resulting in modest changes of expression in a much greater (though still modest) number of genes of far less profound, quantitative influence on phenotype (note that their subtle effects are likely to escape the eyes of both field biologists and experimental geneticists scrutinising mutant screens).

We therefore conclude that saltation theory offers the best explanation for several key issues that have long perplexed evolutionary biologists. Most notably, saltation:

- 1 removes the troublesome mathematical challenge inherent in natural selection of driving an initially very rare mutant allele to fixation in a large panmictic population, by causing instant isolation from the 'parental' population (cf. Bateman, 1999a; Marshall *et al.*, 1999; Shubin and Marshall, 2000);
- 2 thereby provides a simple and credible explanation for the equally mathematically improbable phenomenon of true sympatric speciation without introgression;

- 3 permits a lineage to cross valleys in the fitness landscape that would be lethal to a lineage attempting to make the evolutionary journey gradually, thus immediately reaching at least the higher slopes of another peak and giving natural selection a subordinate role of subsequently assisting that novel phenotype towards the crest of its new-found fitness peak (Bateman, 1999a; Cronk, 2001); in short, saltation is a pre-requisite for radical re-organisation of form;
- 4 accommodates a genuine qualitative difference in degrees of morphological divergence among phylogenetically delimited taxa of contrasting taxonomic ranks (cf. Kellogg, 2002); some newly originated species are trivially morphologically distinct and hence are readily assigned to pre-existing genera, whereas other species originate with sufficiently profound morphological transitions to simultaneously represent previously unknown higher taxa.

The overall contrast between neoDarwinism and supraDarwinian saltation theory (together with the more heterogeneous panoply of parasaltational mechanisms only trivially explored in this chapter but of considerable explanatory power: Table 7.2) is to place greater evolutionary (and systematic) emphasis on the origination of a genetically determined phenotypic novelty and less on its subsequent dissemination through populations; rather, the genetic-phenotypic novelty is seen as constituting an equally novel population. The fate of this prospecies is determined at least in part by the likelihood that the phenotypic novelty will offer one or more serendipitous features that function as pre-adaptations or exaptations (or allow transfer of an essential function) in the environment initially occupied by the novel organism(s).

Whether this changed emphasis constitutes a genuine paradigm shift (Kuhn, 1962), as we predicted in 1994, remains to be seen. For the present, we will simply echo Darwin by appealing for greater 'flexibility of mind' in the light of these fascinating recent developments, not least among the more evangelistic of Darwin's modern disciples.

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